

NATURAL HISTORY OF THE CALIFORNIAN TRAPDOOR SPIDER GENUS *ALIATYPUS* (ARANEAE, ANTRODIAETIDAE)

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ABSTRACT. The antrodiaetid trapdoor spider genus *Aliatypus* is found in a wide range of elevations and habitats, nearly all of which experience the summer drought characteristic of the California Mediterranean climate. All eleven species prefer sheltered, stable, and sloping ground surfaces. Burrows tend to be clustered, sometimes very densely, in favorable sites and are often side-by-side with those of non-congeneric mygalomorphs. Burrows penetrate more or less perpendicular to the ground surface plane, are usually more nearly horizontal and slightly wider at the upper and lower ends, and are lined with silk and a packed soil casing. The shape of the wafer-type trapdoor is relatively constant within each species and differs markedly from one species group to another. *Aliatypus* trapdoor construction behavior differs from the collar-door construction behavior of *Antrodiaetus* only by a simple orientation rule. Entrance sealing with silk or silk plus soil plugs is common in at least some species during the dry summer. For nearly all species, male emergence, mating, and spiderling dispersal occur during the wet fall or winter period. Females oviposit in the summer. The pendulous egg sac is placed in the burrow bottom. Clutch size varies from 8-267; small-bodied species have smaller clutches than large-bodied species. Prey capture resembles that of *Antrodiaetus* but is constrained by the trapdoor hinge. Hypotheses are presented regarding the selective advantage of various traits. It is postulated that a simple genetic change causing a shift from collar-door to trapdoor construction was a key evolutionary event permitting the adaptive shift of the proto-*Aliatypus* lineage into the summer-drought niche which its collar-door-building sister taxa are not able to exploit.

The mygalomorph trapdoor spider genus *Aliatypus* consists of eleven described species, ten living in California and the adjacent edge of Nevada and one living in Arizona (Fig. 1) (Coyle 1974). This is one of the most diverse and abundant of the remarkably numerous burrow-dwelling mygalomorph spider genera living in the California floristic province. *Aliatypus* species live in ravine and road banks and other slopes in a remarkable variety of elevations, climates, and habitats ranging from hot dry creosote bush scrub communities to cool montane red fir forests and wet coast redwood forests.

Aliatypus is most closely related to the collar-door and turret spiders of the genera *Antrodiaetus* and *Atypoides*, which together with *Aliatypus* constitute the Antrodiaetidae, a family whose most probable sister groups (Atypidae and Mecicobothriidae, see Coyle 1971, 1974, 1994; Raven 1985; Eskov & Zonshtein 1990; Coddington & Levi 1991; Goloboff 1993) lack trapdoor-building species. Consequently, some of the specializations *Aliatypus* shares with other trapdoor-building mygalomorphs in the Ctenizidae, Idiop-

idae, Cyrtaucheniidae, and other families are the result of parallel or convergent evolution.

Nearly all of the data we present herein were gathered by us before 1974. It was our intention to publish these *Aliatypus* natural history observations shortly after the revision of the genus was published some 20 years ago (Coyle 1974). Regrettably, other projects have prevented us from completing this goal until now. To conserve print and emphasize the comparative approach, we will not present detailed descriptions of the natural history of each species as was done for *Antrodiaetus* and *Atypoides* (Coyle 1971), but will instead present an overview of the natural history of the genus, calling attention to any species or populations which are exceptional, and summarizing important data for each species in tables and figures. We have tried to arrange the many topics logically, label them clearly, and combine observations with discussion while making it clear which is which.

This paper, although greatly increasing what is known about the biology of this neglected genus (Smith 1908; Coyle 1971, 1986a; Gertsch

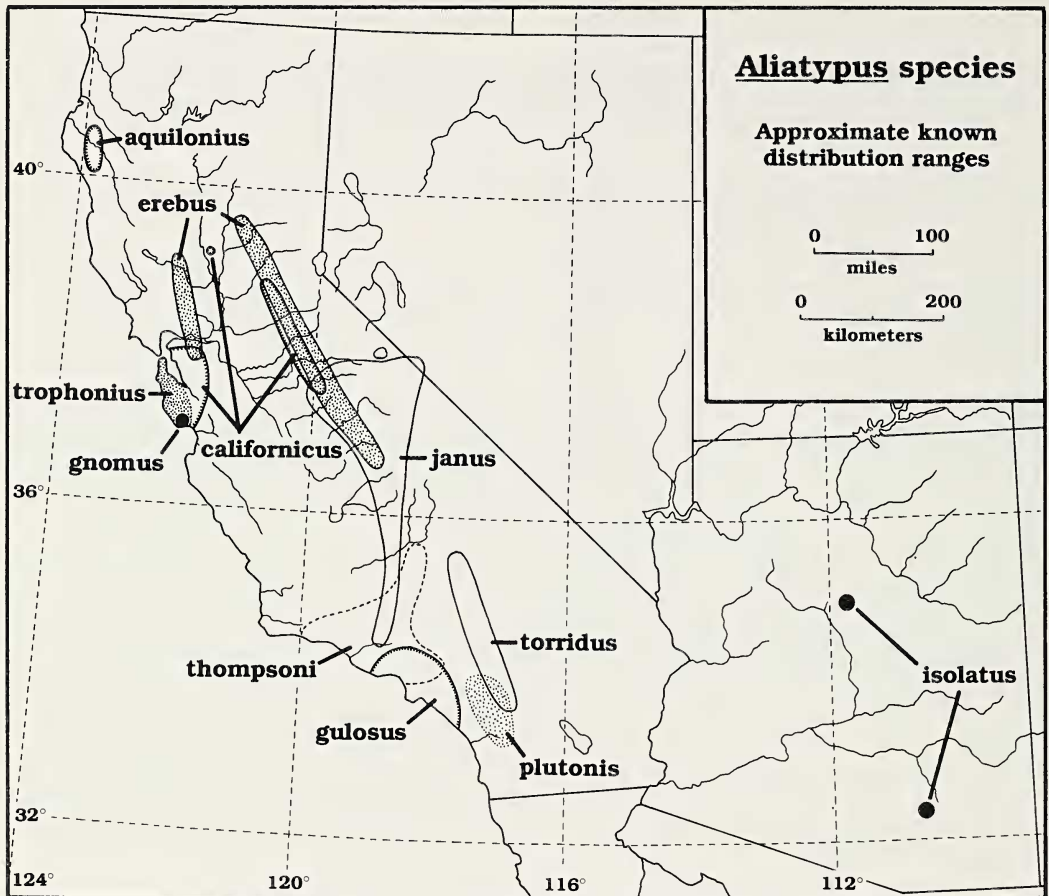


Figure 1.—Map of California, Arizona, and Nevada showing approximate known distribution ranges of the species of *Aliatypus*.

1979), should be considered only a beginning, a foundation of observations and hypotheses which will, we hope, focus more attention on these fascinating spiders. There are a number of unresolved taxonomic problems which deserve closer study in *Aliatypus*; five species (*A. gulosus*, *A. californicus*, *A. janus*, *A. thompsoni*, and *A. erebus*) exhibit particularly marked geographic variation involving some populations which may deserve to be recognized as separate species (Coyle 1974). This paper should be useful to researchers clarifying these issues and others regarding the evolutionary history of the genus. For example, some of the behavioral/ecological characters we describe herein have been used, along with morphological characters, in a modern cladistic analysis of *Aliatypus* species relationships (Coyle 1994) which supports and refines the phylogeny proposed by Coyle (1974) and resolves the polytomy in the *erebus* group by postulating that

A. erebus and *A. trophonius* are sister species and *A. plutonis* and *A. torridus* are sister species. We also hope this paper will encourage and facilitate the conservation of these spiders and their habitats, which are rapidly shrinking due to urban, agricultural, and even recreational development. Regrettably, we have already witnessed the destruction of some demes which we studied in the 1960's and early 1970's.

METHODS

About 95% of the data used in this study was collected by us during many short field trips between 1966 and 1974 (Icenogle) and a seven-week field trip in July and August of 1972 (Coyle). Our collecting methods were described earlier (Coyle 1974). Each spider was given an identification number when it was collected and field notes, photographs, and burrow entrance specimens were keyed to these numbers. Unless noted

otherwise, data on burrow structure are derived from adult female burrows. Although some natural history data, particularly habitat data, were derived from nearly every specimen (about 260 adult females and 80 adult males) and nearly every collecting site listed in the "Records" sections of the revision (Coyle 1974), most of the observations we present in this paper came from the following sites (see Coyle 1974 for complete locality information; number of females collected with broods is in parentheses): *A. gulosus* – Salt Creek (11); coastal *A. californicus* – Alum Rock Park (6), 4.5 mi N Soquel (4), Mt. Loma Prieta (2), Calaveras Reservoir (2); sierran *A. californicus* – Mariposa (5); *A. gnomus* – Henry Cowell Redwoods State Park (4); *A. aquilonius* – Grizzly Creek Redwoods State Park (6), Redway-Briceland (6); *A. janus* – Sequoia National Park (5), Hume Lake; *A. isolatus* – Oak Creek Canyon (2), Santa Catalina Mtns. (2); *A. thompsoni* – Placerita Canyon State Park (5), Chatsworth (5), Henninger Flats (2), Eaton Canyon Park (2), Santa Ynez Mtns. (1), Tehachapi Mtns. (1); *A. erebus* – Wilbur Springs, Mariposa (1), Pinehurst, Nevada City; *A. trophonius* – 4.5 mi N Soquel (5); *A. plutonis* – Univ. of California at Riverside (4), S Banning (1); *A. torridus* – Mountain Center (2), Yucaipa.

Most of the spiders, the burrow entrance specimens, and some of the parasitoids are deposited in the American Museum of Natural History (AMNH). Other spiders are in the Museum of Comparative Zoology at Harvard. The parasitoids and host spiders which are in the second author's collection will eventually be deposited in the AMNH.

The U.S. Weather Bureau records of precipitation which we used covered periods of 20–50 years (depending on the station) between 1900 and 1950. We used records only from 29 weather stations within 50 km of *Aliatypus* collecting localities. Since California is a climatically complex region where striking climatic differences may exist within a transect of a few km (Bakker 1971; Major 1977), the precipitation profiles given in the third column of Table 1 do not accurately represent the conditions experienced by each species, but do, we believe, reliably indicate important *general* differences between the climates experienced by different *Aliatypus* species.

ECOLOGY

Habitat.—Despite its rather small geographic range (Fig. 1), *Aliatypus* occupies a broad range

of elevations (sea level to 3080 m), climates (very arid to moist), and biotic communities (Table 1, Figs. 2–17). All of the California species experience, to one degree or another, the dry warm (to hot) summer and the relatively wet and mild late fall and winter characteristic of California's Mediterranean climate (Major 1977). On average, only 4–15% of the annual precipitation experienced by every California species of *Aliatypus* falls during the five month period of May to September. It is this climate which causes most of these species to be most active during the winter and spring and inactive during at least part of the summer. It is also important to remember that periodic droughts lasting one or more years (with precipitation amounts lower than the averages reported in the third column of Table 1) exert greater than normal stress on these spiders from time to time.

Two species, *A. plutonis* and *A. torridus*, are found in very arid habitats in the interior of southern California (Table 1, Figs. 1, 15–17). *Aliatypus torridus* tolerates the driest and most sparsely vegetated habitats and, not surprisingly, exhibits a strong preference for north-facing slopes and sheltered soil at the bases of large rocks, shrubs, and trees. *Aliatypus gulosus* and *A. thompsoni* are usually found in somewhat less arid habitats in more coastal and montane areas of southern California (Figs. 1, 2, 12, 13). Four other species, *A. californicus*, *A. janus*, *A. isolatus*, and *A. erebus*, live primarily in central California and/or at higher elevations than the aforementioned species and seem to prefer more mesic habitats, primarily woodland and forest communities (Figs. 1, 3, 4, 8–11, 14). Although its habitat range broadly overlaps that of *A. californicus*, *A. erebus* appears to be more tolerant of dryer and colder environments. *Aliatypus janus* is found over an unusually wide range of elevations and is common in the red fir forests of the Sierra Nevada (Fig. 9) where the winters are cold and long; in 1978 its range was extended by the second author, who collected a specimen at 3080 m in the White Mountains near the California-Nevada border. Unlike other *Aliatypus* species, *A. janus* and its sister species, *A. isolatus*, are probably physiologically and/or behaviorally adapted to a colder winter climate, and populations at higher elevations presumably remain inactive during most of the winter. The three remaining species, *A. gnomus*, *A. aquilonius*, and *A. trophonius*, have been found only in the relatively moist redwood forests near the coast of

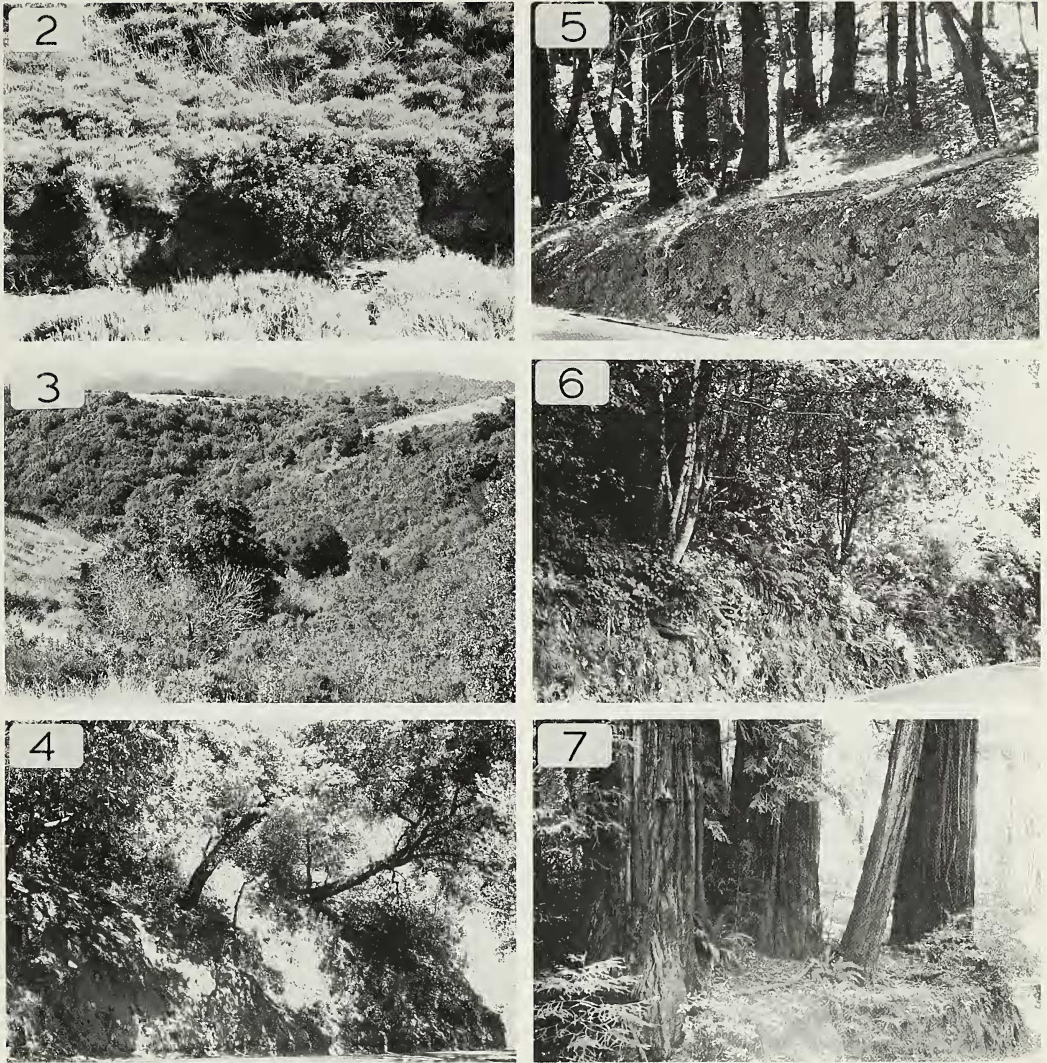
Table 1.—Elevation, precipitation, and habitat data for known populations of *Aliatypus* species. Data in precipitation column are the overall mean and range of the mean annual precipitation records from two or more stations near the localities where each species has been collected (see Methods section). Plant community designation and precipitation (inches) based on Munz and Keck (1959). + means the species occurs in this community type; ++ means the species (because populations are particularly large or common in this community type) may prefer this type. **Aliatypus isolatus*, an Arizona species, is found in canyon woodland, pine-oak woodland, and yellow pine forest communities; the symbols are placed under those California community types which most closely resemble these in physiognomy and precipitation.

Species	Elev. (feet)	Precip. (inches)	Plant community and average annual precipitation									
			Creo- sote bush scrub 2-8	Coastal sage scrub 10-20	Cha- par- ral 14-25	South- ern oak wood- land 15-25	Foot- hill wood- land (open) 15-40	Foot- hill wood- land (dense) 15-40	Yellow pine forest 25-80	Red fir forest 35-65	Red- wood forest 35-100	
<i>gulosus</i>	50-1300	16 13-20		++		++						
<i>californicus</i>	200-2300	32 18-54			+			+	++			++
<i>gnomus</i>	400	41 27-54										+
<i>aquilonius</i>	400	58 38-78										++
<i>janus</i>	1200-10,100	23 13-34							+	++	++	
<i>isolatus*</i>	4400-7500	20 20-21						+	+	+		
<i>thompsoni</i>	900-5400	17 10-25			+	++	++	++	++			
<i>erebus</i>	1100-5400	31 23-49			+			++	++	+		
<i>trophonius</i>	300	34 20-54										+
<i>plutonis</i>	800-3300	13 12-17		+	+							
<i>torridus</i>	2400-4400	10 4-14	+	+	+					+		

central and northern California (Figs. 1, 5-7, 14). The precipitation amounts given in the third column of Table 1 may be lower than the true values for these species and do not take into account the summer fog which boosts the humidity in their forest habitat. It may be that the distinctively small body sizes and consequent high surface-to-volume ratios of these three species (Table 4), as well as their shallow burrows (Table 3), preclude their existence in warmer and dryer habitats, although it should be remembered that even the redwood forests can be quite dry in the summer. The ability of some *Aliatypus* species to survive the periodic fires characteristic of chaparral is demonstrated by our observation of numerous healthy *A. plutonis* and *A. thompsoni*

adults in chaparral localities that had been burned in hot brush fires a year (*A. plutonis*) (Fig. 16) and several months (*A. thompsoni*) earlier. At least some populations of some species encounter occasional flooding; Bentzien (1976) observed that some individuals of *A. californicus* do not abandon rain-flooded burrows and can survive for short periods under water.

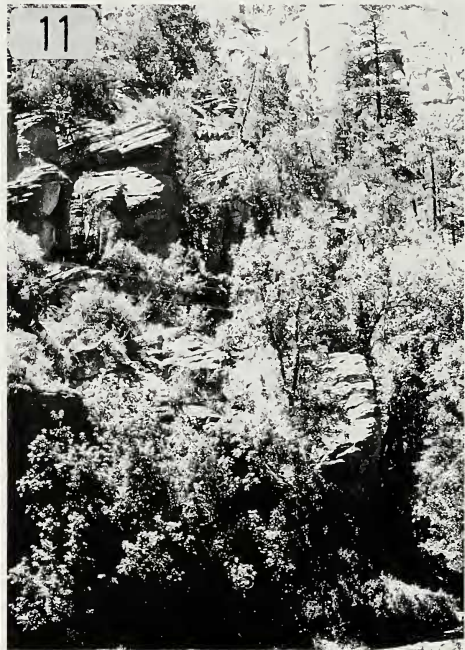
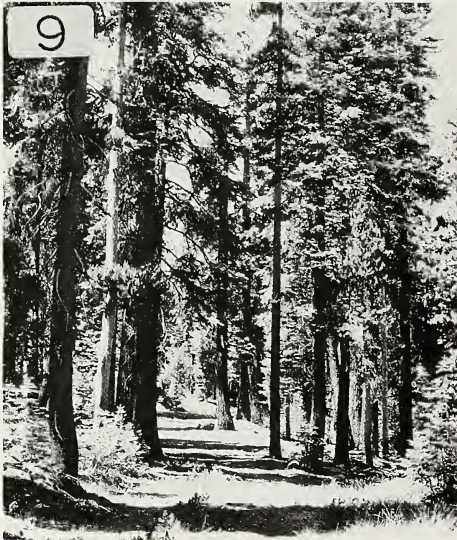
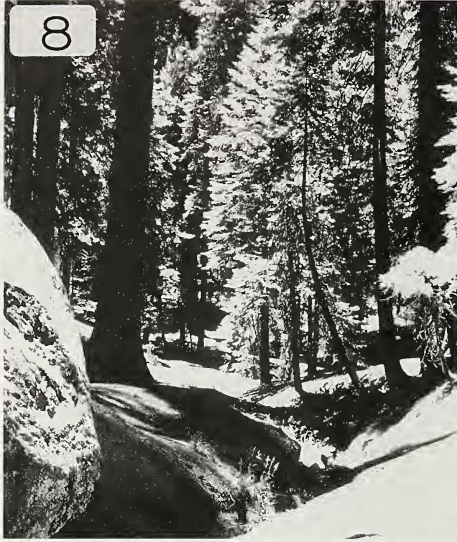
Microhabitat.—All species prefer ground surfaces that are sheltered, relatively stable, sloping, and either north-facing or otherwise shaded. Burrows are seldom found in soil that is subject to erosion, but rather in soil bound together by roots and/or sheltered under protruding roots or rocks. Although most species apparently prefer steep slopes such as ravine or road banks, the four



Figures 2–7.—*Aliatypus* habitat photos. 2, coastal sage scrub habitat at 20 m elev. at Salt Creek, Orange County, California, *A. gulosus* burrows on north-facing stream bank; 3, dense foothill woodland habitat at 700 m elev. at Montebello Rd., Santa Clara Co., California, *A. californicus* burrows on ravine banks shaded by trees; 4, dense foothill woodland habitat at 180 m elev. at Alum Rock Park, Santa Clara Co., California, *A. californicus* burrows on well-shaded north-facing road bank; 5, redwood forest habitat at 120 m elev. at Henry Cowell Redwood State Park, Santa Cruz Co., California, *A. gnomus* burrows on heavily shaded road bank; 6, redwood forest habitat at 120 m elev. at Grizzly Creek Redwood State Park, Humboldt Co., California, *A. aquilonius* burrows on heavily shaded road bank; 7, redwood forest habitat at 120 m elev. at 1.4 mi W Redway, Humboldt Co., California, *A. aquilonius* burrows on low road bank.

erebus group species (*A. erebus*, *A. trophonius*, *A. plutonis*, and *A. torridus*) are usually found on more gentle slopes of 45° or less. In particularly dry habitats, the relatively common occurrence of *Aliatypus* burrows at the base of rock outcrops may be due partly to the tendency of these outcrops to provide runoff, shade, and stability to the adjacent soil. *Aliatypus* species construct bur-

rows in a wide variety of soil types ranging from soft sandy loam and loose pumice to hard clay-loam that is often chunky or rocky. Within some species, *A. janus* in particular, there is much variation in the soil types inhabited. The depth of leaf and/or needle litter cover where burrows are found also varies greatly within the genus and within some species. While occupied banks are

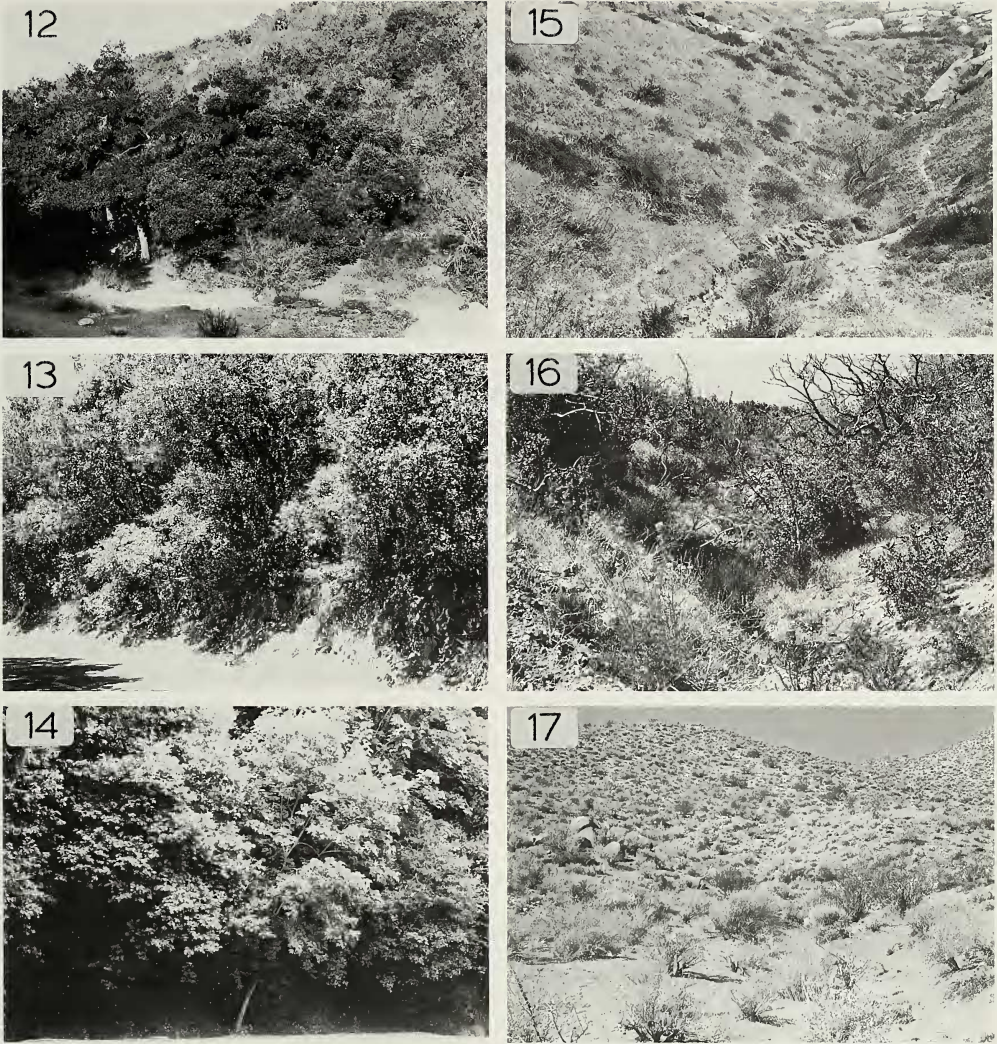


Figures 8–11.—*Aliatypus* habitat photos. 8, yellow pine forest habitat with giant sequoia, white fir, and sugar pine at 2070 m elev. at Sequoia National Park, Tulare Co., California, *A. janus* burrows on bank of small stream; 9, red fir forest habitat at 2450 m elev. at Yosemite National Park, Mariposa Co., California, *A. janus* burrows on and near low road bank (on left); 10, open yellow pine-oak woodland habitat at 1350 m elev. at Manzanita Campground in Oak Creek Canyon, Coconino Co., Arizona, *A. isolatus* burrows on north-facing ravine bank; 11, canyon hardwood-conifer woodland habitat at 1500 m elev. at Cave Springs Campground in Oak Creek Canyon, Coconino Co., Arizona, *A. isolatus* burrows in heavy shade at base of northeast-facing bluff on canyon floor (at bottom of photo).

covered with little or no litter, the gentle slopes inhabited by some species may be covered with up to 8 cm of litter.

Population density.—Populations of *Aliatypus* species usually consist of scattered burrow clusters which vary greatly in area, population density, and distance apart. Sometimes burrow densities may be very high. For example, burrow

entrances of several small juveniles, three large juveniles, and three adult females of *A. gnomus* were crowded together in a 200 cm² area; three adult females and 12 juveniles of *A. californicus* occupied a 1000 cm² area in a large dense population at Alum Rock Park; entrances of some adult females of *A. janus* at Hume Lake were only 5–7 cm apart; and approximately 300 *A.*



Figures 12–17.—*Aliatypus* habitat photos. 12, foothill woodland habitat at Placerita Canyon Park, Los Angeles Co., California, *A. thompsoni* burrows on heavily shaded north-facing ravine bank in oak grove (slope above oak grove covered with chaparral); 13, dense foothill-woodland habitat at 670 m elev. along Stagecoach Road in Santa Ynez Mtns., Santa Barbara Co., California, *A. thompsoni* burrows on shaded road bank; 14, redwood forest habitat at 90 m elev. at 4.5 mi N Soquel, Santa Cruz Co., California, *A. trophonius* and *A. californicus* burrows on heavily shaded road bank; 15, coastal sage scrub habitat at 370 m elev. near Univ. of California at Riverside, Riverside Co., California, *A. plutonis* burrows on 30–80° slopes of ravine banks; 16, chaparral habitat at 1000 m elev. S Banning, Riverside Co., California, *A. plutonis* burrows on northwest-facing ravine bank (at left) under shade of large shrub; 17, creosote bush scrub habitat at 1070 m elev. at NE edge El Paso Mtns., Kern Co., California, *A. torridus* burrows at base of north side of boulders (on left).

thompsoni burrows, including those of several adults, existed in one 3 m² area at Placerita Canyon. This clustered intrapopulation distribution pattern, which is typical of other antrodiaetids (Coyle 1971; Vincent 1993) and many other trap-door spiders (Main 1957, 1976, 1987; Marples 1972), is probably a consequence of the special microhabitat requirements, low dispersal ability,

small prey capture area (Coyle 1986a), and relatively low metabolic rates (Anderson & Pres-twich 1982) of these spiders.

Syntopic burrowing mygalomorph spiders.—*Aliatypus* species are usually syntopic (living side by side) with one or more species of burrowing mygalomorph spiders, species which are potentially their most important competitors. Gen-

Table 2.—Non-congeneric burrow-dwelling mygalomorph spiders known to be syntopic with *Aliatypus* species. *Antrodiaetus* and *Atypoides* are antrodiaetids, *Actinoxia* and *Aptostichus* are cyrtaucheniids, *Hebestatis* and *Bothriocyrtum* are ctenizids, *Calisoga* is a nemesiid, and *Megahexura* is a mecicobothriid (Raven 1985). No such mygalomorphs have yet been found to be syntopic with *A. gnomus* or *A. isolatus*.

	<i>Antro- diaetus pacificus</i>	<i>Atypoides riversi</i>	<i>Actinoxia sp.</i>	<i>Apto- stichus spp.</i>	<i>Hebestatis theveneti</i>	<i>Bothri- ocyrtum califor- nicum</i>	<i>Calisoga longi- tarsus</i>	<i>Mega- hexura fulva</i>
<i>gulosus</i>				+	+			+
<i>californicus</i>	+	+	+	+	+		+	+
<i>gnomus</i>								
<i>aquilonius</i>	+	+						
<i>janus</i>				+	+		+	+
<i>isolatus</i>								
<i>thompsoni</i>				+	+	+		+
<i>erebus</i>		+		+	+		+	+
<i>trophonius</i>		+	+					
<i>plutonius</i>				+		+		+
<i>torridus</i>				+		+		

erally, high elevation *Aliatypus* populations are associated with fewer such syntopic taxa than are populations at lower elevations. As might be predicted from competitive exclusion principles, syntopy with other species of *Aliatypus*—species which should occupy the most similar niches—is relatively rare. Although nine different pairs of *Aliatypus* species are sympatric (Fig. 1), only four sites with clearly syntopic populations of two or more species of *Aliatypus* (only three of the nine possible pairs) have been found, and these (again, in conformance with competitive exclusion principles) do not involve close relatives. *Aliatypus californicus* occurs syntopically with *A. erebus* (at Mt. Diablo and at Mariposa) and *A. trophonius* (at 4.5 mi N Soquel), but has not been found living with its closer relative, *A. janus*. The other congeneric pairing is *A. erebus* with *A. janus* (at Pinehurst). A fourth pair of species, *A. gulosus* and *A. thompsoni*, has been collected in ravines at both Chatsworth and Eaton Canyon Park; however, collecting data, while showing that *A. thompsoni* is much more abundant than *A. gulosus*, are inadequate to determine whether these distantly related species are actually syntopic at these sites. There are, we believe, three areas where additional research is most likely to find added cases of syntopic congeners or interesting patterns of parapatry: 1) In the area near Felton in Santa Cruz County where *A. californicus* and *A. trophonius* are syntopic, *A. gnomus*, which is present in similar redwood forest habitats, much smaller than *A. californicus*

(its putative sister species), and not closely related to *A. trophonius*, may be able to coexist in syntopy with either or both of these species. 2) *Aliatypus thompsoni* and *A. janus*, which live in dense foothill woodland and are not close relatives, may be syntopic in the region around Squaw Flat in Ventura County where they have been found within 1 km of one another. 3) The possible presence of one or two species of *Aliatypus*, in addition to *A. californicus* and *A. erebus*, at or near Mariposa (Coyle 1974) make it a particularly important focus of future studies on the systematics and ecology of *Aliatypus*.

It is more common for *Aliatypus* species to be syntopic with other burrow-dwelling genera than with congeneric species (Table 2). Bentzien (1976) observed that *A. californicus* was syntopic with species in five other burrow-dwelling mygalomorph genera at the University of California Hopeland Field Station in Mendocino County: *Antrodiaetus pacificus*, *Atypoides riversi*, *Aptostichus* sp., *Actinoxia* sp., and *Calisoga longitarsus*. The most diverse association of burrow-dwelling mygalomorphs we have observed with any *Aliatypus* species is at Mariposa, where the following five species (in four families) were common: *A. erebus*, *A. californicus*, *Hebestatis theveneti*, *Calisoga longitarsus*, and *Megahexura fulva*. These mixed species populations of mygalomorphs can be very dense. Near Calaveras Reservoir four adults and 13 juveniles of *A. californicus*, two adults and two juveniles of *Aptostichus*, two adults and six juveniles of *Actinoxia*,

and one *C. longitarsus* adult were collected in one 2 × 4 m area. A 1.2 m² area at Salt Creek contained two adult female and several juvenile *A. gulosus*, eight large juvenile and/or adult female *H. theveneti*, and two adult female *Aptostichus* sp. The burrow entrances of non-congeneric mygalomorph spiders can be remarkably close together; an adult *A. gulosus* entrance was found only 2.0 cm from an adult *Aptostichus* entrance, and another *A. gulosus* entrance was equally close to that of an adult *H. theveneti*. The interactions within these dense mixed species aggregations would be a fascinating topic for study.

Although we seldom noticed microhabitat segregation among the species in these mixed populations of burrow-dwelling mygalomorph genera, observations at other sites suggest some important differences in habitat and microhabitat preferences. *Antrodiaetus pacificus* (Coyle 1971) prefers more humid and cooler habitats than do most *Aliatypus* species. *Bothriocyrtum californicum* commonly inhabits dry, south-facing, gently sloping hillsides or level terrain, places where *Aliatypus* species are rare or absent. *Hebestatis theveneti* exhibits a relatively narrow preference for heavily shaded, very steep firm banks. The habitat/microhabitat preferences of *Aptostichus* species seem to resemble those of *Aliatypus* rather closely except that *Aptostichus* species are more common than *Aliatypus* species in the drier, more southern, localities which harbor both genera. Since *C. longitarsus* and *M. fulva* do not excavate burrows but simply occupy existing cavities and crevices, they primarily inhabit areas in banks where soil is less stable than that preferred by the other (burrowing) taxa. *Aphonopelma*, the only sympatric burrow-dwelling mygalomorph genus which we have not observed living next to *Aliatypus*, prefers sites much like those favored by *B. californicum*.

BURROWS: FORM, FUNCTION, AND CONSTRUCTION BEHAVIOR

Burrow orientation.—*Aliatypus* burrows usually extend into the ground approximately perpendicular to the ground surface or at a small angle downward from this perpendicular (Fig. 18); only occasionally does a burrow slope downward more than 15° from the perpendicular (Fig. 18b, f). This relationship between ground surface slope and burrow slope is typical of other antrodiaetids as well, and is not surprising; this is normally the most efficient route to stable and humid soil layers (Coyle 1971). Usually the up-

per and bottom ends of the burrow are closer to horizontal than is the rest of the burrow (Fig. 18). The burrow is otherwise relatively straight unless there are obstacles such as rocks and roots. The more nearly horizontal orientation of the upper end of the burrow is especially noticeable where the ground surface is not steeply inclined (Fig. 18h, j, k) and is partly responsible for the fact that the plane of *Aliatypus* entrance openings is usually 60–90° and rarely less than 30° above the horizontal. Perhaps these entrance orientation features reduce 1) the effort the spider expends to overcome gravity during the prey capture lunge, and 2) the chance that water or mud will flood into the burrow entrance during heavy rainfall.

Burrow shape and size.—The burrow is circular in cross-section and unbranched. As in most other antrodiaetids (Coyle 1971) and many other burrowing mygalomorphs, the bottom end of an *Aliatypus* burrow is nearly always larger in diameter than the rest of the burrow (Figs. 18, 24, 48), possibly an adaptation to allow space for turning around, manipulating prey, molting, egg sacs, and spiderlings. Typically, except in the case of *A. aquilonius* burrows, the upper end is also enlarged (Fig. 18); this expansion may help accommodate prey handling, turning around, and mating.

Within each species the lengths of adult female and male burrows vary greatly (Table 3). Some of this variation must be the result of spider size and age variation. Note that penultimate and adult males, which are smaller and often younger than many adult females, usually have shorter burrows. However, the correlation between female burrow length and body size is weak, at best, within each species (correlation coefficient = -0.99–0.86 for burrow length vs. carapace length) and within the combined sample of all species (0.57 for burrow length vs. carapace length, 0.45 for burrow length vs. the cube of carapace length). Environmental factors, such as the hardness, stability, moisture content, and temperature of the soil probably also play a role in determining burrow length. The three small-bodied species, *A. gnomus*, *A. aquilonius*, and *A. trophonius*, have significantly shorter burrows ($P < 0.01$) than all the other, larger species (Fig. 18). One factor, in addition to small mass and a high body surface to volume ratio, which may prevent these small *Aliatypus* species from inhabiting warmer and drier habitats like those frequented by many of their larger congeners, is that they

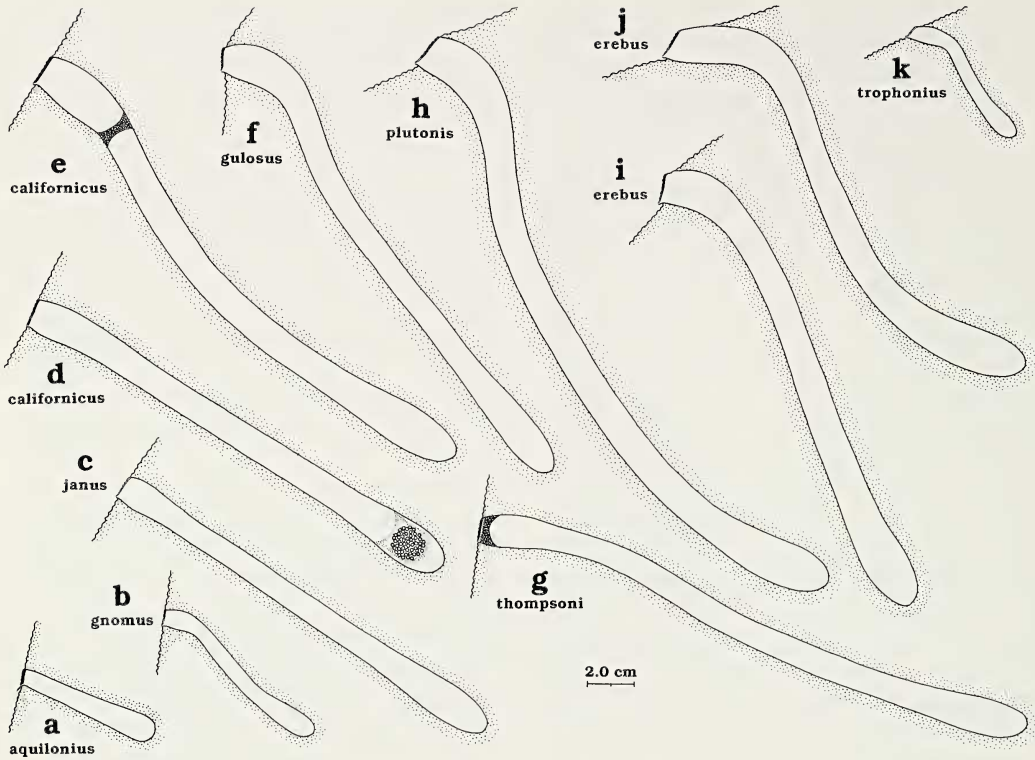


Figure 18.—Representative profiles of adult female burrows of nine *Aliatypus* species, drawn to scale. Burrow d (*A. californicus*) contains an egg sac, burrow e (*A. californicus*) a type C closure, and burrow g (*A. thompsoni*) a type B closure.

would have to expend a disproportionate amount of energy in order to excavate and maintain burrows that are long enough to protect them from overheating and desiccation in the dehydrated surface soil. *Aliatypus plutonis* tends to construct the longest burrows; female burrows of this species are significantly longer ($P < 0.01$) than those of four (*A. gulosus*, *A. californicus*, *A. janus*, and *A. erebus*) of the six *Aliatypus* species of equal or larger body size. Perhaps the disproportionately long burrows of *A. plutonis* help prevent overheating and desiccation in the especially warm and dry environments inhabited by this species. Presumably for similar reasons, the longest *Aliatypus* burrow we have excavated, a 51 mm long *A. torridus* burrow, was in the driest *Aliatypus* site we have found, a creosote bush desert habitat in the El Paso Mountains; adult *A. torridus* burrows in the wetter pine forest at Mountain Center were less than half that long. Although heat and drought presumably exert selection pressure on older juveniles and adults of all *Aliatypus* species, such pressure is probably much greater on earlier

instars because of their larger surface-to-volume ratios and shorter burrows. An examination of the drought-inflicted mortality and rate of burrow excavation in these early instars would be instructive.

Silk lining of burrow.—All *Aliatypus* burrows are lined with silk, which presumably provides some reinforcement and may help conserve water. The thickness of this lining varies within an individual burrow, within a population, and among the different species. In many species (*A. californicus*, *A. gnomus*, *A. isolatus*, *A. thompsoni*, *A. plutonis*, and *A. torridus*) burrows possess throughout most of their lengths only a very thin, almost imperceptible, layer of silk (Figs. 24, 46, 47), much thinner than that of most other Californian trapdoor spiders. Usually the silk lining is thickest in the upper end of the burrow, and may be especially thick if the surface substrate is loose or dry. This probably serves to discourage the collapse of this part of the burrow, which is usually in the least stable, most erosion-prone substrate, and may also reduce the loss of water

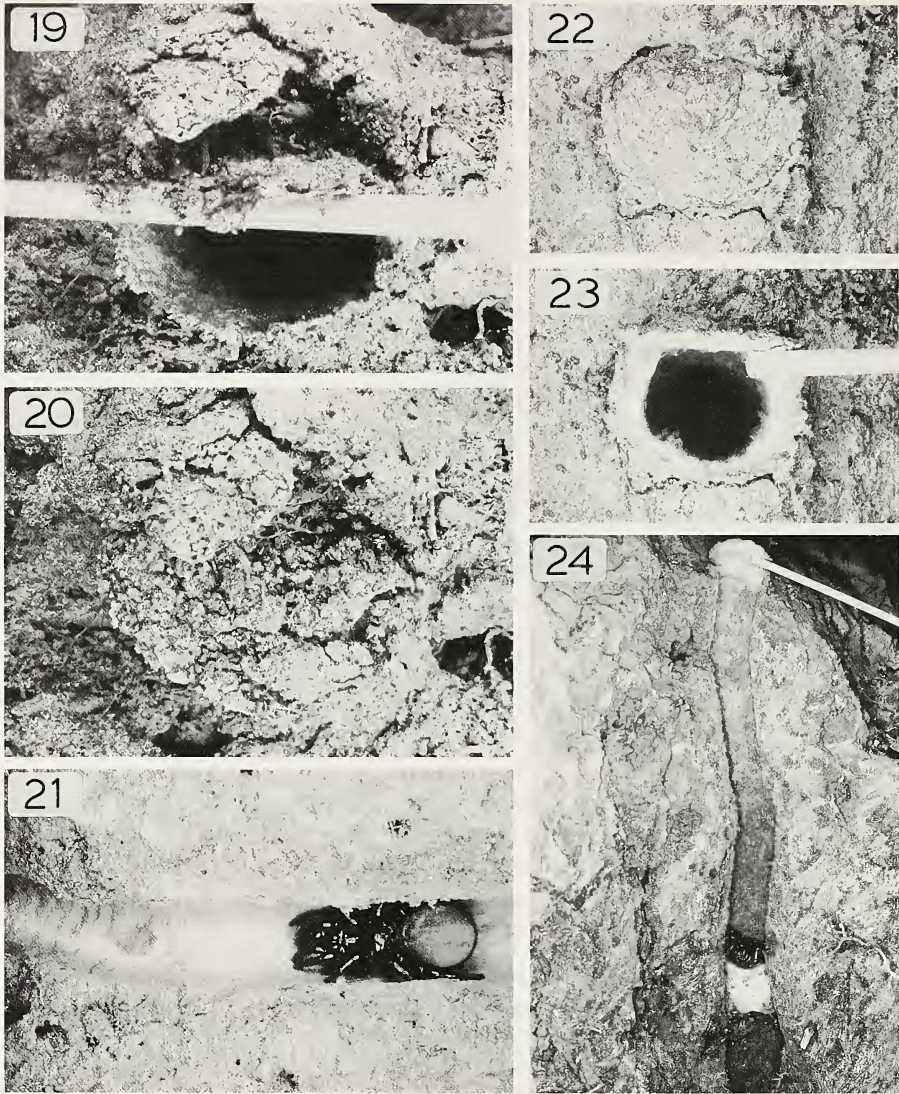
Table 3.—Burrow and trapdoor dimensions of *Aliatypus* species. All data from burrows of adults. Range, mean, and standard deviation given for samples of four or more. Sample size in parentheses after range; sample sizes for trapdoor shape and hinge indices are same as for trapdoor width. Trapdoor shape index = width/height; trapdoor hinge index = width/hinge length (Fig. 38).

	Female burrow length (cm)	Female burrow midpoint diameter (mm)	Male burrow length (cm)	Female trapdoor width (mm)	Female trapdoor shape index	Female trapdoor hinge index
<i>gulosus</i>	12–30 (11) 23.2 ± 6.2	9–16 (11) 11.5 ± 2.4	11, 12	14–16 (4) 14.5 ± 1.0	1.56–1.78 1.66 ± 0.12	1.07–1.27 1.15 ± 0.10
<i>californicus</i>	13–33 (24) 21.2 ± 4.9	10–15 (14) 12.9 ± 1.6	10–25 (10) 14.2 ± 4.9	11.5–16 (6) 14.3 ± 1.8	0.96–1.25 1.18 ± 0.11	1.07–1.25 1.17 ± 0.07
<i>gnomus</i>	7–9.5 (3) 8.3	6, 7	4–7 (3) 5.0	8–9.5 (3) 9.0	1.19–1.27 1.23 ± 0.04	1.06–1.19 1.13 ± 0.07
<i>aquilonius</i>	3.5–13 (16) 6.1 ± 2.8	6–12 (16) 8.9 ± 1.7	3.5–6 (3) 4.5	6–13 (14) 8.8 ± 2.2	1.08–1.31 1.18 ± 0.08	1.00–1.30 1.17 ± 0.07
<i>janus</i>	11–30 (12) 18.7 ± 5.4		9–21 (4) 15.0 ± 5.2	14–18 (5) 16.2 ± 1.5	1.20–1.33 1.28 ± 0.05	1.06–1.08 1.07 ± 0.01
<i>isolatus</i>	14–30 (8) 22.1 ± 6.3	10–11 (4) 10.8 ± 0.5	6–13 (4) 8.3 ± 3.2	12, 13	1.18, 1.20	1.09, 1.13
<i>thompsoni</i>	16–41 (20) 25.9 ± 6.7	9–15 (15) 11.3 ± 1.8	9–16 (7) 14.6 ± 2.5	10.5–15 (15) 12.4 ± 1.2	1.05–1.36 1.19 ± 0.09	1.08–1.44 1.22 ± 0.11
<i>erebus</i>	15–30 (12) 21.3 ± 4.4	11–17 (9) 13.8 ± 2.6	12–15 (4) 12.8 ± 1.5	19–23 (8) 20.5 ± 1.2	1.31–1.67 1.49 ± 0.13	1.28–2.00 1.59 ± 0.30
<i>trophonius</i>	4–7 (5) 5.1 ± 1.1	7–9 (3) 6.3	3, 4	9, 10	1.29, 1.67	1.43, 1.80
<i>plutonius</i>	18–45 (9) 32.1 ± 8.9	12–16 (7) 14.8 ± 1.6	12–23 (5) 17.0 ± 4.4	14–21 (7) 16.0 ± 2.5	1.33–1.55 1.42 ± 0.08	1.25–1.42 1.37 ± 0.06
<i>torridus</i>	15–51 (7) 25.1 ± 12.3	11–14 (6) 12.7 ± 1.4	5–22 (4) 14.5 ± 7.6	17	1.55	1.31

vapor into the drier surface substrate. Often the lower end of the burrow is also relatively well lined with silk. *Aliatypus trophonius* and especially *A. erebus* construct a markedly thicker silk lining than other *Aliatypus* species (with the exception of some *A. gulosus* females). The entire lining of an adult female *A. erebus* burrow is a tough grey-white to white silk that is much thicker than that in syntopic *A. californicus* and *A. janus* burrows.

Burrow wall.—The walls of most of the burrows of many *Aliatypus* species are made smoother and harder than the surrounding soil, probably by packing the soil when it is moistened by rain and possibly by a “saliva,” as has been observed in some other trapdoor spiders (Monks 1886; Eddy 1948; Main 1976; Gertsch 1979). This design feature, much like the silk lining, probably functions to stabilize the burrow walls and/or increase water vapor retention in the less stable, dryer surface substrate. At least most of the *A. isolatus* burrows located in especially dry

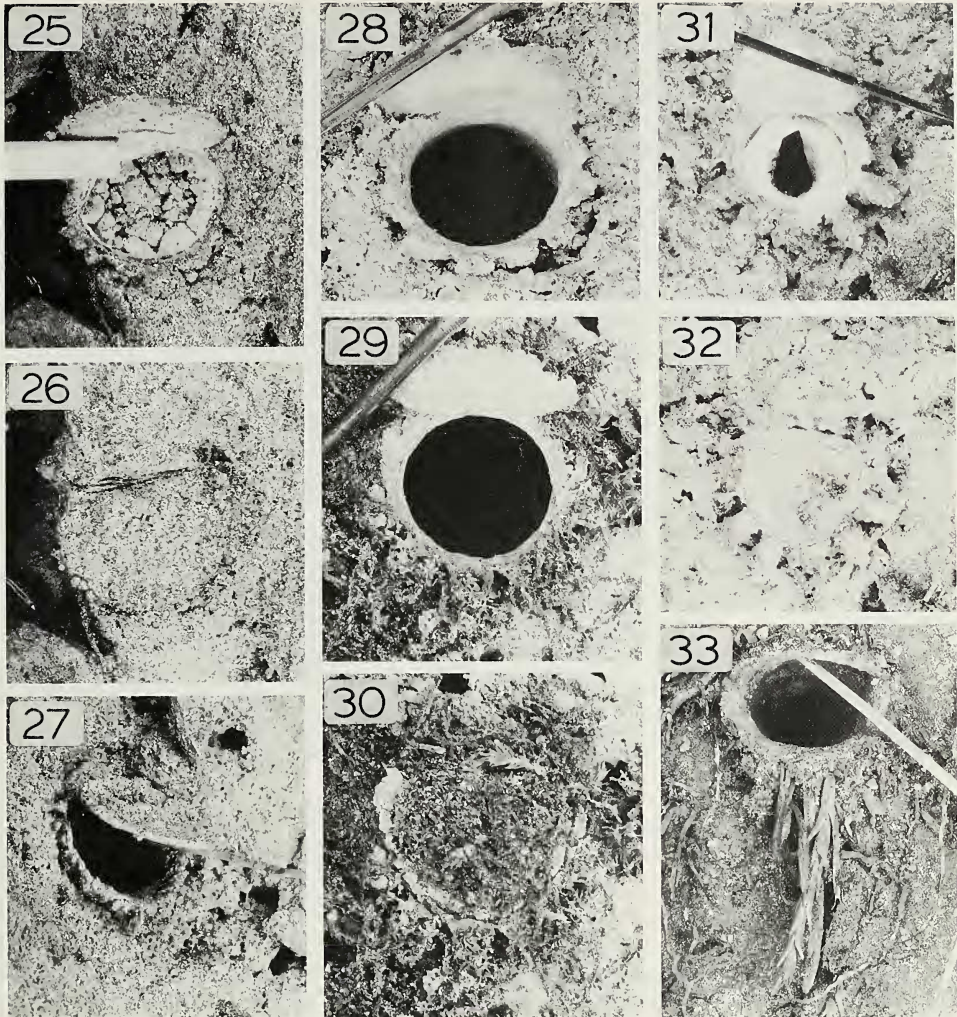
habitats were lined in their upper several centimeters with an almost cement-like casing surrounded by markedly looser soil. Sometimes, at least, this casing is soil that has been excavated from the burrow bottom and, rather than being discarded from the burrow entrance, is packed into the burrow wall. For example, the upper two-thirds of an *A. californicus* burrow in soft dark loam was lined with a 1–3 mm thick hard-packed layer of light sandy clay into which the lower one-third of the burrow penetrated. In some *A. thompsoni* burrows, faint outlines of discs of dried mud that had been plastered onto the walls were visible. Although species with the thickest silk lining (*A. erebus* and *A. trophonius*) appear to rely little on packed mud to reinforce their walls, many of the species living in the driest habitats (*A. isolatus*, *A. thompsoni*, *A. plutonis*, and *A. torridus*) have only a very thin silk lining but well-developed wall casing; they appear to rely heavily upon packing and “plaster” for wall reinforcement and/or water retention.



Figures 19–24.—*Aliatypus* burrows and entrances. 19, *A. gulosus* burrow entrance with door propped open, Salt Creek, Orange Co., California; 20, same *A. gulosus* entrance as in Fig. 19 showing closed door and small old door above and to left; 21, *A. gulosus* female in exposed burrow, Salt Creek, Orange Co., California; 22, sealed entrance of *A. californicus*, 4.5 mi N Soquel, Santa Cruz Co., California; 23, same entrance as in Fig. 22 after forcing door open to expose silk seal; 24, same burrow as in Fig. 23, exposed and photographed from below showing female on top of egg sac in defensive position.

Entrance rim.—The silk-lined entrance rim flares out to form a lip against which the door fits snugly (Figs. 19, 28, 33, 35, 36). Sometimes this lip is elevated slightly above the surrounding substrate (Fig. 27), usually 1–3 mm in *A. plutonis*. In *A. erebus* the rim is often elevated 2–4 mm and flares out generously so that the lip is about 2 mm wide. In contrast, the entrance rim of *A. thompsoni* is almost never elevated above the surrounding soil (Figs. 39, 40). One striking fea-

ture of *A. aquilonius* entrances is that at least 90% of all adult burrows have tough tabs of silk and soil (sometimes including pieces of moss) which are extensions of and radiate out from the ventral and lateral sectors of the entrance rim (Figs. 28–32). These entrance rim tabs vary in number from three to six and in length from 1–5 mm. Touching the tip of a tab triggers an accurate prey capture response; perhaps these tabs serve to extend the spider's prey sensing radius

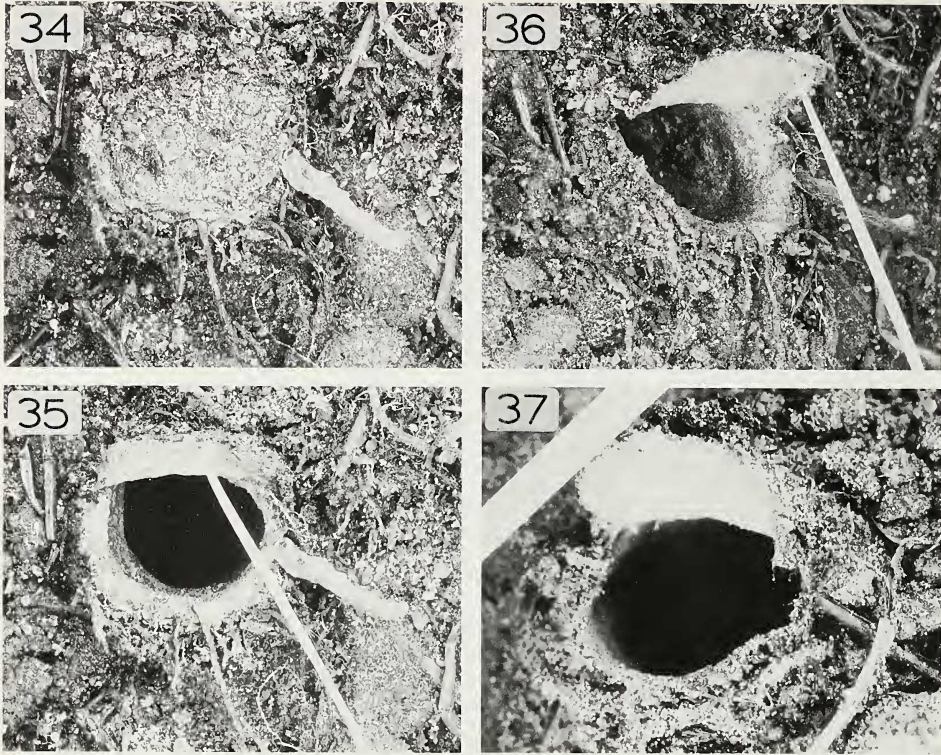


Figures 25–33.—*Aliatypus* burrow entrances. 25, entrance of *A. gnomus* with door forced open to show thin silk seal and soil plug, Henry Cowell Redwood State Park, Santa Cruz, California; 26, same entrance as in Fig. 25 with door sealed shut; 27, *A. gnomus* door propped open, Henry Cowell Redwood State Park, Santa Cruz, California; 28, *A. aquilonius* door propped open, silk plus soil tabs on entrance rim, Grizzly Creek, Redwood State Park, Humboldt Co., California; 29, *A. aquilonius* entrance with door propped open, with tabs of silk plus moss on rim, Grizzly Creek, Redwoods State Park, Humboldt Co., California; 30, same entrance as in Fig. 29, door shut; 31, *A. aquilonius* entrance with door forced open to show heavy silk seal, with silk plus soil tabs on rim, 1.4 mi W Redway, Humboldt Co., California; 32, same entrance as in Fig. 31 before door opened; 33, *A. janus* entrance with door propped open and linear litter attached to rim, Sequoia National Park, Tulare Co., California.

(Coyle 1986a). The only other *Aliatypus* species observed to attach materials to the entrance rim is *A. janus*; about 25% of the entrances at the Sequoia National Park and Hume Lake sites had elongate pieces of plant material attached to the entrance rim (Figs. 33–36). These pieces, usually fir needles and redwood leaves up to 20 mm long, were attached firmly by their ends to the rim at irregular intervals, but were most numerous at

the ventral sector of the entrance. The possibility that these pieces of linear litter extend the prey sensing radius of *A. janus* was not tested.

Trapdoor form.—The edge of the closed trapdoor extends slightly beyond the entrance rim so that the rim is not normally visible (Figs. 20, 26, 32, 34, 42). The hinge is positioned at the uppermost sector of an inclined entrance such that gravity causes the door to shut automatically.



Figures 34–37.—*Aliatypus* burrow entrances. 34, *A. janus* entrance with linear litter attached to rim, Sequoia National Park, Tulare Co., California; 35, same entrance as in Fig. 34 with door propped open; 36, same as in Fig. 35 in side view; 37, *A. isolatus* entrance with door propped open, Cave Springs Campground, Oak Creek Canyon, Coconino Co., Arizona.

The hinge axis, although sometimes straight, is often slightly curved and consequently resists being opened much beyond an angle of 60°. This is a particularly noticeable feature of *A. gulosus* and *A. plutonis* doors (Fig. 38). Sometimes, particularly in the *erebus* group, the corners of the door at each end of the hinge extend well beyond the hinge so that the functional hinge is not as wide as it appears from the outside (Fig. 38). Door size of adult females (Table 3) varies considerably within and among species, but, not surprisingly, is much more strongly correlated with body size than is burrow length. The correlation coefficient of door width vs. carapace length ranges from 0.42–0.95 among the species. Door shape is surprisingly constant within each species and differs markedly between species and groups of species (Table 3, Fig. 38). *Aliatypus erebus* and its three close relatives (*A. trophonius*, *A. plutonis*, *A. torridus*) all have similarly shaped doors which are proportionally broader (width/height = 1.29–1.67, mean = 1.46 ± 0.12; width/hinge

length = 1.25–2.00, mean = 1.49 ± 0.24) than the doors of *A. californicus* and its four close relatives (*A. gnomus*, *A. aquilonius*, *A. janus*, *A. isolatus*) (width/height = 0.96–1.33, mean = 1.20 ± 0.08; width/hinge length = 1.00–1.30, mean = 1.15 ± 0.07) (Fig. 38, Table 3). The *A. gulosus* door is proportionally broad like that of the *erebus* group but has a proportionally broad hinge as in the *californicus* group (Fig. 38); its high hinge length/door height (1.22–1.67, mean = 1.46 ± 0.18) distinguishes it from all other species (0.71–1.25, mean = 1.02 ± 0.12). *Aliatypus thompsoni* doors are shaped much like those of the *californicus* group species.

All *Aliatypus* species possess relatively thin (wafer-type) doors. Most doors are composed of silk and soil, and often, on the outer surface, bits of moss or dead plant debris from the surrounding ground surface, so that they are often camouflaged visually and perhaps tactually (Figs. 30, 39). Sometimes one or two small (old) doors remain attached above the functional door at the

hinge (Fig. 20). Door thickness and stiffness vary within the genus. Most species have doors 1–2 mm thick (in center) that are flexible to semi-stiff. Two species, *A. aquilonius* and *A. thompsoni*, have somewhat thicker (1–2.5 mm thick) doors which are quite stiff (Figs. 28–32, 39, 40). The doors of *A. aquilonius*, although small, are particularly thick and rigid, with slightly beveled edges, and therefore approach the cork-type door form of some trapdoor spiders. The stiffness of an *Aliatypus* door is determined not only by its thickness but also by its composition. If, as is the case for some *A. erebus* and *A. trophonius* individuals, the door contains little or no mineral soil and is composed instead of silk and plant litter/humus fragments, it is very light weight and flexible. The silk, which is relatively non-elastic, is always concentrated on the undersurface of an *Aliatypus* door. As a result, a thin door may bend rather readily if pushed up from the center of the undersurface but, if its outer surface is composed of a non-compressible layer of soil, is much more resistant to bending when pushed down from the center of the top surface. Consequently the door, even when not very thick, may be an effective barrier to agents that press inward against it.

Burrow construction behavior.—Sporadic observations of four large captive *A. isolatus* juveniles on a horizontal soil surface indicate that first, as in *Antrodiaetus* (Coyle 1971), a shallow enclosure or cell is constructed, later the trapdoor is formed, and then, under the protection of the door, the burrow is lengthened. Close and fairly constant observation of one of these spiders during the cell construction phase revealed three of the four behavior patterns used by *Antrodiaetus* for cell construction (Coyle 1971). The dominant pattern was excavating; burrowing and silk application (on the rim of the cell) were performed less frequently; raking was not observed. We were not able to observe cell closure or trapdoor construction. The distribution of the soil that was subsequently excavated from the bottom of the lengthening *A. isolatus* burrows indicates that these spiders do not catapult each excavated pellet of soil as do some ctenizid and idiopid trapdoor spiders (Passmore 1933; Coyle 1981; Coyle et al. 1992), but instead reach out from the entrance and drop it; this excavated soil, mostly in the form of pellets 2–4 mm in diameter, accumulated in a relatively large pile (15–18 mm tall, 30–40 mm diameter, and with center 10–20 mm from threshold) close in front of each entrance threshold on the horizontal soil surface. In mid-

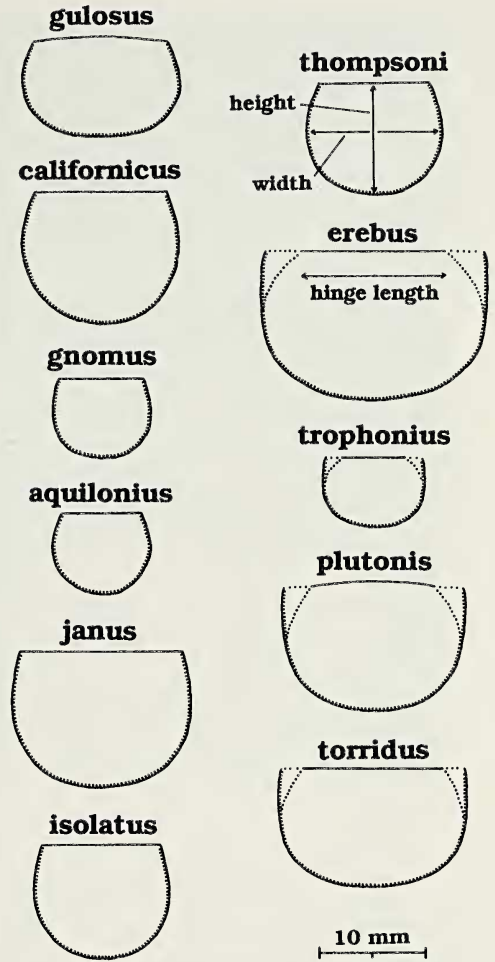
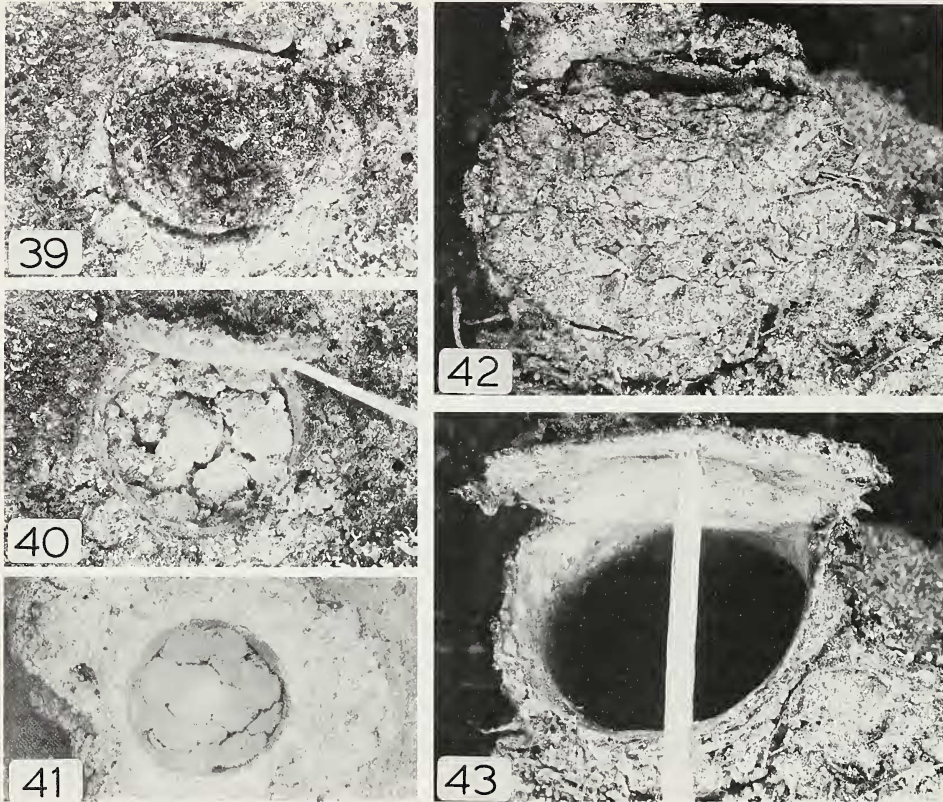


Figure 38.—Outline drawings of adult female door shapes of *Aliatypus* species using mean dimensions given in Table 3 for each species; dotted lines for the four *erebus* group species illustrate how the doors of these species often extend laterally beyond the ends of the hinge so that the functional hinge may be markedly shorter than it appears from outside.

October many *A. janus* burrows at Hume Lake and one *A. erebus* burrow south of Shaver Lake were observed with deposits of freshly excavated soil extending downhill from the ventral sector of the entrance rim, soil that had obviously been dropped, not catapulted.

Mayo (1988) found that entrance construction in *A. thompsoni* requires two to several hours and involves the following sequence of behaviors: A wad of soil is dug by biting into the bottom of the burrow with the chelicerae, which then carry this soil with the help of the pedipalps as the spider backs up the burrow. Just inside



Figures 39–43.—*Aliatypus* burrow entrances. 39, *A. thompsoni* entrance, Henninger Flats, Los Angeles Co., California; 40, same entrance as in Fig. 39 with door forced open to show thin silk seal and soil plug; 41, inside view of hard flattened mud pellets forming plug against door of *A. thompsoni*, Stagecoach Road, Santa Ynez Mtns., Santa Barbara Co., California; 42, *A. plutonis* entrance (after removal from burrow), S Banning, Riverside Co., California; 43, same entrance as in Fig. 42 with door propped open.

the entrance, the spider pivots to face out the entrance and then tests the shape of the rim by tapping along a sector of the rim with pedipalp and leg I tarsi until a depression is detected. It then releases its soil load on the entrance rim by extending (lifting) its chelicerae and flexing and extending its pedipalps. The soil load is then pressed into the rim with the front (rastellar) surfaces of the chelicerae while all four pedipalp and first leg tarsi pull soil from outside the entrance rim and compress it against the chelicerae; this rim molding activity is usually repeated a few times with slight shifts to the right and/or left. Then the spider pivots 180° and applies silk to this area of the rim before descending to the burrow bottom and repeating the sequence just described. After building a reinforced rim around the entire entrance with numerous repetitions of this sequence, the spider then begins releasing and molding soil and applying silk almost exclu-

sively at the dorsal (upper) sector of the entrance rim. This extends the dorsal sector rim into a flap and eventually a completed door. Door shape testing, soil release on the edge of the developing door, and the door molding behavior replace and are virtually identical to rim shape testing, soil release on the rim, and rim molding. Periodically, during the latter stages of door construction, the door's fit is tested by pulling it down to the entrance opening and tapping at gaps between the door edge and entrance rim with pedipalp and leg I tarsi. Apparently, additional silk and soil are added to the "completed" door periodically over the course of several days, but such activity was difficult to observe. This door construction behavior is very similar in both form and sequence to the trapdoor construction behavior observed in some ctenizids and idiopids (Coyle 1981; Mayo 1988; Coyle et al. 1992). This door molding method also appears to be used by

the Mesothelae, and may therefore, as suggested by Coyle et al. (1992), be the plesiomorphic mode of door construction in the Mygalomorphae.

Mayo (1988) discovered that *A. thompsoni* trapdoor construction behavior differs remarkably little from the behavior *Antrodiaetus unicolor* uses to construct its collar-door. The form and sequence of the behavior units are essentially the same in both taxa; the striking difference in door form is the result of a simple orientation difference – whereas, after an initial period of entrance rim construction, *Aliatypus* directs nearly all of its construction behavior at the dorsal sector of the rim (and the flap/door that consequently develops there), *Antrodiaetus* continues instead to distribute its efforts evenly to all sectors of the entrance rim and therefore produces a continuous collapsible collar. Mayo pointed out that only a simple genetic change affecting the neural mechanism controlling the spider's orientation just prior to rim shape testing and soil release would be sufficient to shift the construction product from a collar to a trapdoor or *vice versa*. It follows that the evolutionary shift from collar-door construction, which is probably the primitive state in antrodiaetids, to trapdoor construction in proto-*Aliatypus* may have been rapid (Coyle et al. 1992). In spite of their distinctive appearance, trapdoors, at least in the antrodiaetids, are simply collars with one sector hypertrophied and the rest reduced.

Entrance sealing behavior.—A large proportion of individuals of at least some *Aliatypus* species seal their burrow entrances during the dry summer. This is certainly true for *A. californicus* (24 of 28 entrances examined were sealed), *A. gnomus* (8 of about 12), *A. aquilonius* (23 of about 50), and *A. thompsoni* (all 41 were sealed). Observations indicate that *A. gulosus* and *A. plutonis* may be much less prone to seal their entrances, but the data is scanty for these and other *Aliatypus* species.

Three different types of entrance seals have been observed in the genus. One common sealing strategy (type A) involves a silk seal (Figs. 22, 23, 31, 32, 48). The door is held tightly shut by a relatively dense layer of silk applied to the undersurface of the door and the burrow wall adjacent to the door. This silk seal is continuous around the entire circumference of the door and is thinner to non-existent in the center of the door undersurface. Considerable force is necessary to pry the door up and away from this seal. Another common type of entrance seal (type B)

consists of a silk seal (similar to, but thinner than, that just described) plus a hard plug of soil pellets packed up against this silk and the undersurface of the door and adjacent wall surface (Figs. 18g, 25, 26, 39–41). The spider obviously first seals the door shut with silk and then presses (probably with the front of the chelicerae) moist excavated soil pellets up against the door-wall juncture and the door. The plug thus formed is concave on its inner surface, which exhibits the outlines of the individual flattened pellets. These plugs range from 0 to 6 mm thick in the center and are correspondingly thicker peripherally; sometimes the plug is quite thin or even open in the center if no soil has been attached to the middle of the door undersurface. The third entrance sealing strategy (type C) has been observed only in the Mariposa population of *A. californicus*. All six entrances observed in this population had unsealed doors, but a hard soil plug was found 13–50 mm (mean = 28.7 ± 12.9) below the door (Fig. 18e), usually where the burrow narrowed. This plug is thickest peripherally where it is attached to the wall; both upper and lower surfaces are concave. The center thickness of these plugs ranged from 1–6 mm (mean = 3.0 ± 1.9). In at least two of these Mariposa burrows, delicate strands of silk had been spun irregularly across the burrow lumen between the door and the plug.

Four species (*A. aquilonius*, *A. erebus*, *A. trophonius*, and *A. plutonis*) have been observed to construct only type A closures. Two species (*A. gulosus* and *A. thompsoni*) have been observed to construct only type B closures. *Aliatypus gnomus* and *A. isolatus* construct both type A and type B closures, although *A. gnomus* appears to construct predominantly type B. *Aliatypus californicus* is the only species we have found to construct all three types of entrance closure, but 65% of the entrance closures observed in this species were type B. Entrance sealing is apparently less common in most *Antrodiaetus* and *Atypoides* species and usually involves only a thin silk seal, but at least two species, *Antrodiaetus pugnax* and *Antrodiaetus stygius*, employ soil plugs similar to the type B closure of *Aliatypus* during dry periods (Coyle 1971).

It is probable that entrance sealing in *Aliatypus* serves more than one function, but some evidence indicates that the primary function is water conservation. Smith (1908) found that none of the coastal *A. californicus* entrances he observed were sealed during the wet season from late December to April, but that during the rest of the

year entrances were sealed unless they were in especially humid sites like redwood forest stream banks. We have found sealed entrances only during the drier months of the year. Differences observed on August 7 and 8, 1972, between the Redway-Briceland and Grizzly Creek populations of *A. aquilonius* also support this hypothesis. The percentage of sealed burrows at Redway-Briceland (100%, $n = 20$), where the soil was relatively dry, the spiders small (Coyle 1974), and the adult female burrows shallow (mean = 4.0 ± 0.4 cm, $n = 7$), was significantly greater than at Grizzly Creek (10%, $n = 30$) where the soil was not so dry, the spiders larger, and the burrows deeper (mean = 7.9 ± 2.6 cm, $n = 9$). It seems likely that the type B closure is more effective at preventing water loss than is the type A closure. This is especially true in cases where the sealed door has been torn off by some agent. Sixteen *A. thompsoni* burrows were observed with missing doors but all of these burrows had intact soil plugs and living occupants. Entrance sealing, especially the soil plugs of closure types B and C, may also serve as a deterrent to predators and parasites.

The general tendency for *Aliatypus* females with broods and especially for molting spiders to have sealed entrances is also consistent with the idea that entrance sealing serves primarily to reduce body water loss, because both spiderlings (with their high surface to volume ratio) and molting spiders are especially prone to rapid water loss. Entrance sealing during the dry summer by brooding females and juveniles is a standard anti-desiccation adaptation of trapdoor spiders living in arid regions (Hutchinson 1904; Passmore 1933; Main 1957, 1978, 1987; Buchli 1969). In at least some *Aliatypus* species (*A. californicus*, *A. gnomus*, *A. aquilonius*, and *A. thompsoni*), oviposition, hatching, and development to the second instar occur typically within the protection of a sealed burrow during the hot dry summer period—a season unfavorable for other activities (feeding, mating, dispersal, burrow construction)—and in time for the brood to emerge and disperse in the wet fall or winter activity period. However, the sealing of burrows containing broods is not obligatory; some or all of the brooding females we observed in the following species had unsealed entrances during the dry season: *A. gulosus*, *A. aquilonius*, *A. janus*, *A. isolatus*, and *A. plutonis*. Moreover, two of these *A. aquilonius* females were observed to be in foraging postures at their burrow entrances on the night of August 8.

Burrow repair behavior.—The ability to quickly respond to burrow entrance damage during the dry season by constructing a temporary closure has been observed in *A. thompsoni*. A juvenile whose burrow entrance was removed spun a thin silk septum across the open end of the burrow within several minutes. Another spider, 30 min after the upper end of its burrow had been removed, had plugged the opening with a large number of dry dirt pellets which it had bound together with silk. This spider could be seen carrying, with its chelicerae, pieces of soil (which had probably fallen down the burrow when the upper end was destroyed) and pushing them into this plug. A similar entrance closure was constructed in the laboratory by a penultimate male which had been living in an open burrow; this spider subsequently molted to adulthood. We observed in the field several other instances of temporary plug construction in response to entrance destruction. Such behavior may serve to reduce the infiltration of soil, water, and animals, and to reduce the danger of desiccation.

LIFE HISTORY AND REPRODUCTIVE BIOLOGY

General life history.—Like other antrodiaetids (Coyle 1971) and probably all other mygalomorph spiders, *Aliatypus* species have life cycles of more than one year, and adult females may live for years. We do not have enough data to estimate reliably the generation time for any species of *Aliatypus*, but we do predict that the large-bodied species require at least two years more to reach maturity than do the smallest-bodied species. As data presented below indicate, mating in all species of *Aliatypus* (with the possible exception of *A. isolatus*) occurs in fall or winter, eggs are fertilized and deposited in the following summer, and the spiderlings developing from these eggs disperse from the maternal burrow that fall. Whereas adult males cannot molt or continue to grow or construct burrows, and therefore probably never survive to a second mating season, adult females are capable of molting and reproducing for two or more years (iteroparous), as evidenced by the wide range of brooding female body sizes within many populations. Main (1987) has emphasized that this combination of female longevity, iteroparity, and the long period (>2 years) required for males to reach adulthood should boost the chances of successful reproduction in very dry environments

where reproduction may be prohibited during years of extreme drought.

Molting.—All recently molted *Aliatypus* spiders whose entrances were observed had their entrances sealed, indicating that molting, as in other antrodiaetids (Coyle 1971), typically occurs in sealed burrows. This is not surprising considering a spider's vulnerability to desiccation and predators while molting. Molting takes place near the bottom end of the burrow, as evidenced by the fact that all intact exuviae found ($n = 9$) were facing toward the entrance resting upright on the ventral sector of the burrow wall 10–30 mm above the bottom end. Fragmented exuviae were often found packed into the very bottom end of burrows. Adult males do not fragment their exuviae as thoroughly or pack them as tightly into the burrow bottom as do females or juvenile males; indeed some males may do nothing to their last exuvium.

Male maturation and emergence.—Penultimate males are readily recognized by their swollen pedipalpal tarsi. One observation indicates that these may even be swollen in the ante-penultimate instar; an *A. californicus* male collected at Mariposa in October 1969 with swollen pedipalpal tarsi and kept in soil in a jar molted to the penultimate instar in July 1970 and then to adulthood in October 1971. Since the spider consumed only two houseflies while in captivity, and these only after the 1970 molt, it is possible that abnormally low food intake delayed maturation and created an extra "penultimate" instar. The rearing to adulthood of a few males collected in the penultimate instar indicates that this instar normally lasts about a year in the larger-bodied *Aliatypus* species.

As in other antrodiaetids (Coyle 1974), there appears to be strong selection for male *Aliatypus* emergence and wandering to coincide with rainy weather. The males of most *Aliatypus* species molt to maturity in very late summer and early fall and then emerge from their burrows in fall and/or winter to wander in search of mates during the rainy season (Fig. 44). Although the data are not abundant, at least some males of *A. janus* and its sister species, *A. isolatus*, may mature earlier in the summer and emerge to mate earlier than other species, before the onset of the cold winters that the high elevation populations of these species experience. This tendency of high elevation populations to breed earlier than their low elevation relatives has been observed in other antrodiaetids (Coyle 1974). While the males

of some species, such as *A. gulosus*, *A. californicus*, and *A. erebus*, may emerge at the onset of the rainy season in late fall, in species such as *A. thompsoni*, *A. plutonis*, and *A. torridus* emergence may be delayed until the peak of the rainy season in January and February. This later emergence may be due to the fact that these three species live in especially dry climates where only the peak rainfall months may provide enough moisture for wandering males. The vulnerability of adult *Aliatypus* males to dryness, even within their own burrows, is suggested by the discovery at Las Barras Canyon on 12 October 1972 (an exceptionally dry year) of three dead (and partly dried) and only two living *A. thompsoni* males in their burrows.

Courtship and mating behavior.—*Aliatypus* males, like most other mygalomorph males and unlike females, possess traits (like proportionally longer legs and better developed tarsal scopulae) which presumably enhance their ability to travel overland (Fig. 45). The following observations of *A. gulosus* adult males suggest that while searching for mates, *Aliatypus* males may survive for several weeks, possibly without feeding, and may travel considerable distances, that they may be aided in this search by a female-produced contact (or very short range olfactory) pheromone associated with the female burrow, and that once he discovers the female's burrow entrance, the male may signal to the female with substrate vibrations. One male collected while it was wandering survived in captivity for 53 days without accepting available food and spent most of its last 30 days walking in a terrarium. Another male, released on two separate occasions into jars where adult females had constructed burrows without doors, "pawed" excitedly at these burrow entrances with its pedipalps and front legs (but the females responded aggressively). Yet another male, released in a jar with a female burrow possessing a full-formed trapdoor, "pawed" excitedly around the trapdoor, but the female did not respond. We suspect that, as in other antrodiaetids (Coyle 1971), the males of *Aliatypus* search for mates primarily at night.

Although we have not observed *Aliatypus* mating behavior, Coyle (1971) developed a hypothesis about its form on the basis of an observation of mating behavior in *Atypoides riversi* and a comparative analysis of the morphology of the male first legs, pedipalps, and chelicerae in the Antrodiaetidae. Males of *Atypoides* and *Antrodiaetus*, like most mygalomorph males, possess

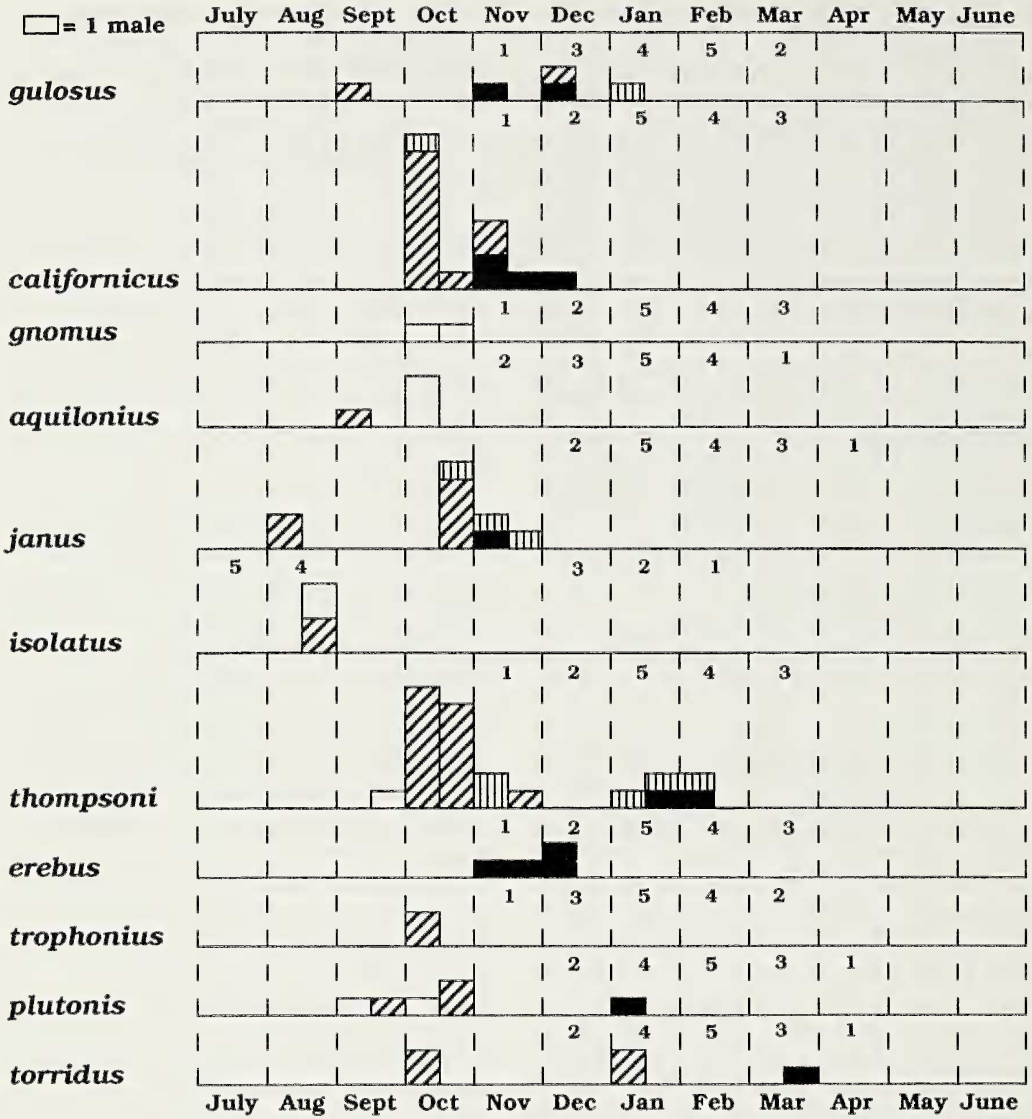
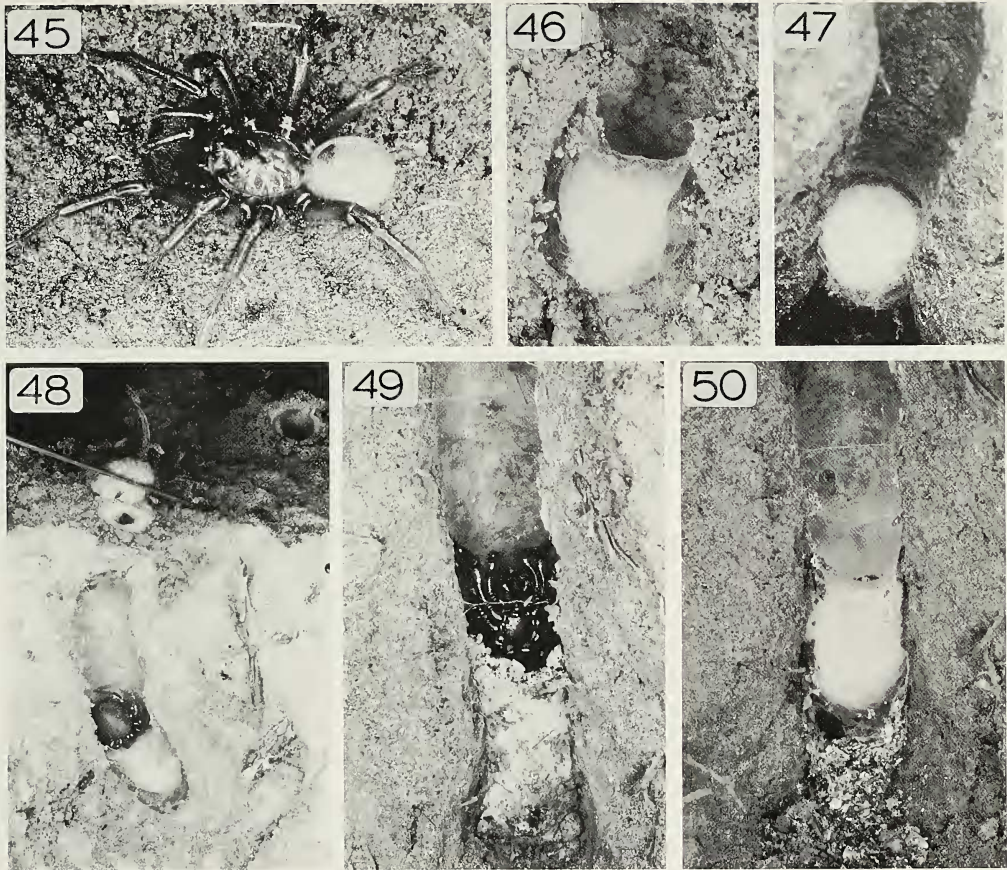


Figure 44.—Timing of male maturation and wandering in *Aliatypus* species as represented by frequency histograms of all available adult male collection dates. Records grouped into half month periods. Diagonal stripes represent adult males collected before exiting from their burrows. Solid black represents adult males collected after leaving their burrows. Vertical lines represent adult males collected either before or after abandoning their burrows; inadequate data with specimen. Empty rectangles represent dates on which penultimate males molted to maturity in captivity. Numbers indicate the five wettest months ranked from 1 (least wet) to 5 (wettest).

pedipalps of moderate length and mating claspers (chelicerapophyses in *Atypoides*, leg I structures in *Antrodiaetus*) which hold the female to help position the partners for palpal insertion and protect the male from attack (Coyle 1971, 1986b). The unusually elongate pedipalps of *Aliatypus* males, in concert with an absence of mating claspers, suggests that these males copulate

by contacting the female only lightly and at a distance with the first legs, and use their long pedipalps to reach the unusually great distance to her genital opening. We further suggest that by forgoing the practice of lifting the front of the female – a practice widespread among mygalomorphs with mating claspers – this hypothesized strategy might permit copulation within the bur-



Figures 45–50.—*Aliatypus* male and egg sacs. 45, adult male of *A. janus* from Yosemite National Park, Mariposa Co., California; 46, bottom of *A. gnomus* burrow with egg sac, Henry Cowell Redwood State Park, Santa Cruz Co., California; 47, top view of *A. californicus* egg sac showing how it occludes burrow lumen, same burrow as in Fig. 24; 48, exposed burrow of adult female *A. aquilonius* with egg sac, door forced open to show silk entrance seal, photographed from below, 1.4 mi W Redway, Humboldt Co., California; 49, bottom end of exposed *A. gulosus* burrow with female in defensive position above egg sac, Salt Creek, Orange Co., California; 50, same burrow as in Fig. 49 with soil and outermost silk peeled away to expose egg sac and prey remains packed into very end of burrow.

row and thereby reduce the chance of being detected by predators. We predict that other trap-door spiders with such atypically long male pedipalps – some *Actinopus* species (Koch 1842), *Stasimopus robertsi* Hewitt (Hewitt 1916), *Heteromigas terraereginae* Raven (Raven 1984), and *Plesiolenia bonneti* (Zapfe) (Zapfe 1961; Goloboff & Platnick 1987), to name examples from three families – will also be found to lack mating claspers and employ a copulation strategy similar to that hypothesized for *Aliatypus*.

Oviposition and egg sac structure.—Egg sacs have been observed in all *Aliatypus* species except *A. janus*, *A. eribus*, and *A. trophonius*, and are remarkably similar in form and placement

throughout the genus. The brief description of *Aliatypus* egg sacs given by Coyle (1971) is mostly erroneous, having been based upon fragmentary field notes and egg sacs preserved in alcohol. Unlike the semi-lenticular egg sac of *Antrodiaetus* and *Atypoides* which is broadly attached to the burrow wall 0.4–0.8 of the distance down the burrow, the *Aliatypus* egg sac is a pendulous bag attached to the burrow wall in the bottom part of the burrow so that its bottom end is suspended 2–50 mm (usually less than 20 mm) above the end of the burrow (Figs. 18d, 24, 46–50). Both the deeper placement of the *Aliatypus* egg sac (in the coolest and most humid part of the burrow) and its structure may be adaptations to prevent

Table 4. Clutch (brood) size, egg diameter, and female carapace length of *Aliatypus* species. Only clutches which were complete (all eggs or spiderlings were collected) are used in this table. Ten eggs measured per brood. Adult female carapace length data from Coyle (1974); range, sample size (in parentheses), mean, and standard deviation given.

	Clutch size			Egg diameter (mm)			Carapace length (mm)
	<i>n</i> (broods)	Range	Mean and SD	<i>n</i> (broods)	Range	Mean	
<i>gulosus</i>	8	58-180	106.0 ± 45.4	2	1.18-1.37	1.31	4.8-7.7 (27) 6.07 ± 0.65
<i>californicus</i>	16	49-267	115.6 ± 58.9	3	1.33-1.52	1.40	5.4-8.0 (44) 6.66 ± 0.68
<i>gnomus</i>	4	14-29	23.0 ± 6.5	1	1.22-1.41	1.32	3.5-4.2 (4) 3.77
<i>aquilonius</i>	12	8-64	24.7 ± 18.7	4	1.07-1.33	1.18	2.8-5.9 (26) 3.96 ± 0.84
<i>janus</i>							5.1-8.9 (25) 6.62 ± 0.92
<i>isolatus</i>	3	63-73	68.7 ± 4.2	3	1.22-1.55	1.44	4.6-8.3 (10) 5.71 ± 1.05
<i>thompsoni</i>	10	64-233	124.6 ± 48.7	7	1.15-1.67	1.42	4.8-7.9 (66) 6.28 ± 0.60
<i>erebus</i>	1	195					6.2-10.0 (24) 7.78 ± 1.01
<i>trophonius</i>	4	23-58	33.8 ± 14.4				3.5-5.2 (10) 4.38 ± 0.55
<i>plutonis</i>	4	70-104	84.0 ± 14.9				6.0-7.9 (8) 6.68 ± 0.53
<i>torridus</i>	2	122, 136	129.0	1	1.26-1.44	1.37	5.5-6.5 (8) 6.10 ± 0.32

desiccation and overheating of the eggs and spiderlings. The sac is slightly narrower than the burrow lumen and is as long or longer than it is wide. It is suspended by a multitude of fine silk lines attached to the surrounding wall surface on all sides. The upper part of the egg sac is covered by a concave lid of silk that spans and occludes the burrow lumen and thus might act in part as a moisture barrier to help maintain higher humidity in the burrow bottom around the developing brood. If the middle of this lid is grasped with forceps and pulled up and away from the sac, it parts rather easily and cleanly from the bag portion of the sac and exposes the eggs contained in the bag. This indicates that the spider first constructs the open-topped bag in position just above the burrow bottom, places the eggs in it from above, and then spins a sheet of silk across the burrow lumen against the top of the egg cluster and the bag. So the behaviors involved in building this sac are basically the same as those *Antrodiaetus* and diplurids use (Coyle

1971, 1988); it is basically a lenticular (ancestral) sac that has been reoriented about 90° to span the burrow lumen and has become much thicker. The egg sac silk appears completely homogeneous both in color and texture. Captive *Aliatypus* females, like those of other mygalomorphs we have kept in captivity (*Aptostichus*, *Bothriocyrtum*, *Aphonopelma*, and *Thelechoris*), sometimes consume their eggs, which may be a common response of iteroparous females to recycle eggs that are either threatened by unfavorable conditions or have not been fertilized (Passmore 1933; Baerg 1958; Willey & Coyle 1992).

Fecundity and egg size.—All data on the timing of brood development (Fig. 51) are consistent with the conclusion that *Aliatypus* females produce no more than one clutch per year. Since in some populations we found large numbers of non-gravid broodless adult females alongside females with broods, and since it is unlikely that all of these broodless females were newly adult and approaching their first breeding season, it is

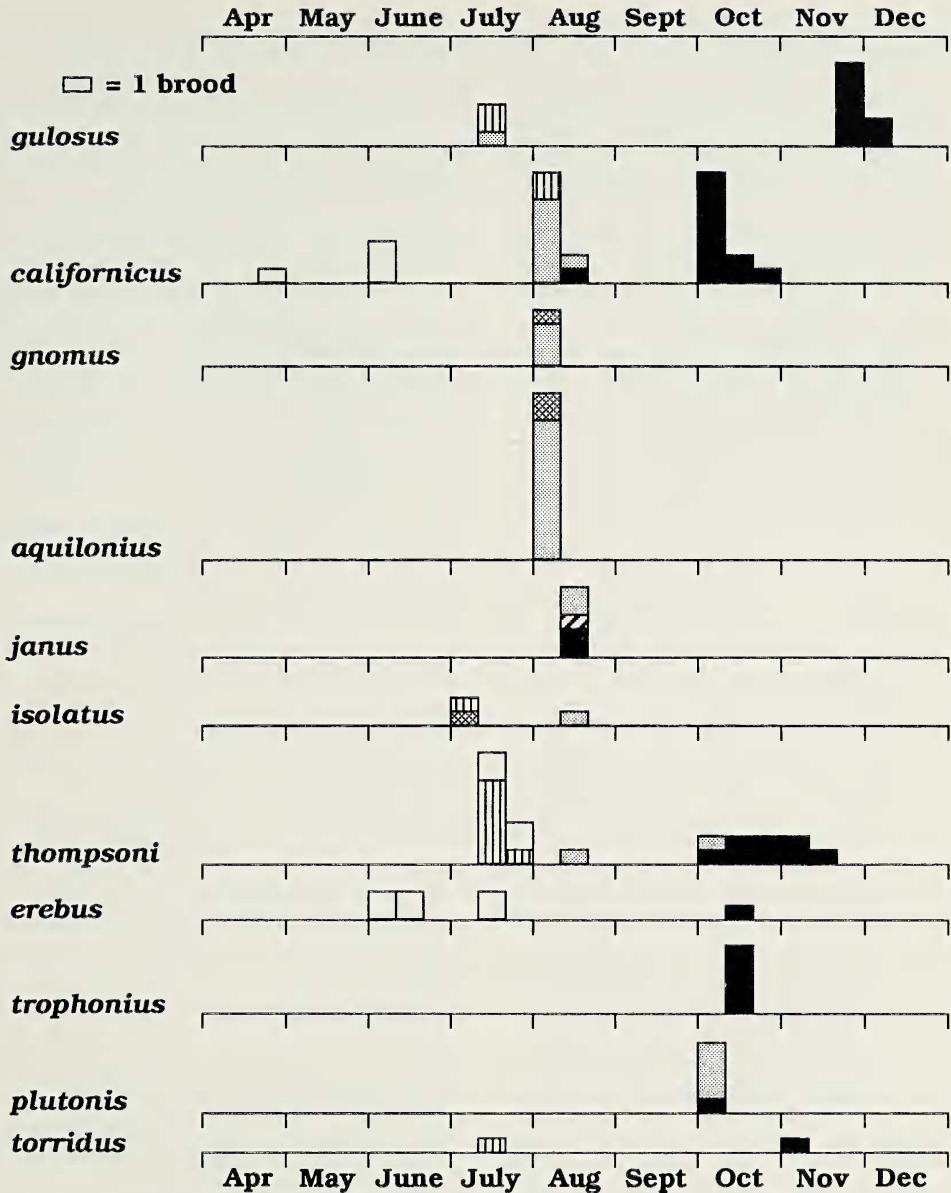


Figure 51.—Timing of brood development in *Aliatypus* species as represented by frequency histograms of collection dates of broods and gravid females. Records grouped into one-third month periods. Empty boxes represent gravid females (those with developing eggs readily visible through the abdominal wall). Vertical lines represent egg sacs with eggs. Cross-hatching represents broods that are hatching. Stippling represents first instar broods. Diagonal stripes represent broods with both first and second instar spiderlings. Solid black represents second instar broods.

probable that adult females sometimes forgo reproduction during a year, perhaps even reproducing every other year, as does the Australian trapdoor spider *Anidiops villosus* (Rainbow) (Main 1978). Table 4 presents the clutch and egg size data for the ten *Aliatypus* species that have yielded such data. Clutch size varies widely with-

in each of the four species represented by sample sizes of eight or more. The correlation between carapace length and clutch size is very weak (0.27–0.42) in three of these four species, indicating that, within species, factors such as nutritional state are often better predictors of reproductive output than is body size. The exceptional species,

A. aquilonius, exhibits strong congruent geographic variation in body size and clutch size; the Grizzly Creek sample has significantly ($P < 0.01$) larger females with significantly larger clutches (20–64, mean = 37.5 ± 18.9 , $n = 6$) than the Redway-Briceland sample (8–18, mean = 11.8 ± 4.4 , $n = 6$).

When all species are assessed together, the correlation between carapace length and clutch size is stronger (0.77); the three small-bodied species (*A. gnomus*, *A. aquilonius*, and *A. trophonius*) have significantly smaller broods than do the large-bodied species ($P < 0.01$). It appears that small adult body size has evolved independently in each of these three species (Coyle 1994). Presumably selection for small body size caused a large reduction in clutch size (and probably fecundity) because of the reduced biomass available in a small body for egg production and because of constraints limiting selection for reduced egg volume. The scanty data suggest that one of these small species, *A. aquilonius*, may have evolved slightly smaller eggs than some species (*A. californicus*, *A. isolatus*, and *A. thompsoni*; $P < 0.01$) and thereby boosted its fecundity. It is tempting to suggest that this shift may have been permitted by the beneficial (compensatory) effects of the wetter climate and thicker doors characteristic of this species on the survivability of these smaller spiderlings, which because of their higher surface to volume ratio, would be particularly prone to desiccation. While an extension of this argument would predict selection for eggs larger than the genus norm in species like *A. torridus* which live in very dry habitats, the limited data (Table 4) do not conform to this prediction. Clutch and egg sizes of *Aliatypus* species are comparable to those of *Antrodiaetus* and *Atypoides* species (Coyle 1974), but quite different from those of the arid-adapted Australian aganippine trapdoor spiders (Main 1957). Even though they are equally large or larger spiders, the aganippines have much smaller clutches (11–127) than do the medium to large size *Aliatypus* species, in part, at least, because aganippine eggs are much larger (mean diameter = 1.87–4.14 mm).

Pattern and timing of early postembryonic development.— Postembryonic development in *Aliatypus* follows the same pattern as in *Antrodiaetus* and *Atypoides* (Coyle 1971). This conclusion is based upon close examination of all *Aliatypus* broods collected, including any accompanying shed chorions, embryonic cuticles, and exuviae. The dark egg teeth, segmentation, and

appendages of the late embryo are visible through the chorion. During hatching, first the chorion splits anteriorly and begins to peel back over the abdomen, then the embryonic cuticle splits, and finally the chorion and cuticle are shed together, remaining attached to one another. The relatively few broods (four) preserved in the process of hatching and the fact that fewer than 10% of the individuals in each of these broods were actually in the process of shedding the chorion or embryonic cuticle, indicate that the hatching process is brief. The embryonic cuticle is very thin and transparent, lacks setae, has blunt, non-functional chelicerae, and possesses a dark, sharp egg tooth at the base of each pedipalp. The first instar spiderling [= “first free postembryonic stage” of Holm (1954), “deutovum” of Yoshikura (1955, 1958), “second postembryonic stage” of Galiano (1972)] which emerges from beneath the embryonic cuticle possesses several tarsal setae, has no rastellum, has conical rudimentary fangs with two or three sharp subterminal projections, has one spinneret spigot on the ventral surface of each posterior lateral spinneret [Coyle (1971) previously overlooked the homologous spigots present in first instar *Antrodiaetus unicolor* spiderlings (Bond 1994)], is unpigmented except for slowly developing pigment around the eyes, and can move about only slowly. The second instar spiderling has fully functional appendages, a rastellum, functional fangs, numerous spinneret spigots, abundant setae, and body pigmentation. It can move about quickly, spin a dragline, construct a burrow and trapdoor, and presumably even capture prey.

Data shedding light upon the timing of brood development in *Aliatypus* species are summarized in Figure 51. The few broods found in the process of molting indicate that molting, like hatching, is a short-lived process for individual spiderlings and is closely synchronized within a brood. It appears that females are gravid (with developing cream-colored eggs visible through the ventral abdominal wall when alive) during the spring and summer, eggs are laid in June or July (often within sealed burrows), and nearly all broods have developed to the second instar by mid-October if not earlier.

Spiderling emergence and dispersal.— The following observations indicate that *Aliatypus* spiderlings may be dependent upon assistance from the mother to escape from the egg sac: 1) An *A. torridus* egg sac was reared in captivity in isolation from its mother, and although the eggs developed to fully sclerotized second instar spi-

derlings, the spiderlings did not emerge. 2) In the Sequoia National Park population of *A. janus*, two females were collected with first instar broods already outside of the egg sac despite appearing ill-equipped to force their way out of an egg sac. 3) In early October two egg sacs containing first instar spiderlings were observed hanging loosely from the walls of an *A. thompsoni* and an *A. plutonis* burrow; these sacs must have been manipulated by their mothers. 4) In all those *Aliatypus* burrows we have examined that had broods which had emerged from the egg sac, the sac was either totally destroyed or pushed flat against the bottom of the burrow, indicating that the mother grossly manipulates the sac soon after, if not during, spiderling emergence.

Not enough collecting was done in the winter months to indicate clearly when the second instar spiderlings abandon the parental burrow, but it is probable that for most species this occurs during the wet season in late fall and winter when the danger of desiccation is low and the soil is moist and soft enough for burrow construction. This would be consistent with Main's (1957) findings that the spiderlings of arid-adapted aganippine trapdoor spiders disperse right after the onset of the rainy season. The discovery of several incomplete second instar *A. gulosus* broods (with fewer than 30 spiderlings each) inside unsealed maternal burrows in November and December, during the early part of the wet season, supports this conclusion. Evidence suggests that *A. janus* broods, especially those at higher elevations, may disperse even earlier; on August 14 at Sequoia National Park only six (second instar) spiderlings were found remaining inside an unsealed maternal burrow, and no spiderlings were found in any of the adult female *A. janus* burrows collected during October and November at several localities. Dispersing and constructing burrows before the cold winter weather experienced by the higher elevation populations of this species differs from the strategy of second instar *Antrodiaetus unicolor* spiderlings, which overwinter in the protection of the maternal burrow and disperse in the spring (Coyle 1971). We have seen no evidence that *Aliatypus* spiderlings ever remain in the maternal burrow beyond the first dispersal season, as do broods of some other trapdoor spiders (Buchli 1969; Marples & Marples 1972; Main 1976; Icenogle pers. obs.).

It is not likely that *Aliatypus* spiderlings balloon, for, as is also the case in other antrodiaetids (Coyle 1971), *Aliatypus* burrows tend to be ag-

gregated and small juvenile burrows are often numerous within 20 cm of adult female burrows. Mygalomorphs which balloon, like some atypids, *Ummidia*, and *Missulena*, exhibit much less burrow clustering (Coyle 1983, 1985; Main 1987; Schwendinger 1990). When removed from their mother's burrow and placed on soil in captivity, *A. thompsoni* second instar spiderlings ran quickly, spun draglines at least part of the time, and constructed burrows with trapdoors 2 mm wide.

FEEDING BEHAVIOR

Prey capture behavior.—Field observations of prey capture in *A. aquilonius* and laboratory observations of prey capture in *A. californicus*, *A. isolatus*, and *A. thompsoni* living in burrows built in captivity indicate that the foraging posture and prey capture response of *Aliatypus* are similar in form to that described for *Antrodiaetus* (Coyle 1971, 1986a). Capture-ready spiders, which we have observed only in the evening and at night, are positioned just inside the entrance with their venters close to the ventral-most sector of the burrow wall and with the tarsi of the pedipalps and legs I and II resting on the entrance rim just inside the slightly opened door. Like *Antrodiaetus* (Coyle 1971, 1986a), *Aliatypus* detect and locate prey only on the basis of substrate vibrations generated by the prey and sensed by mechanoreceptors; vision and chemoreception are not involved. Sometimes a strike can be elicited from a spider that is behind a completely closed door. *Aliatypus* strikes are triggered only when the prey (or another vibration generator) is within 5 mm of the entrance rim. Often the prey must touch the rim or door edge before the spider will strike. During the capture response, the spider lunges out of the entrance toward the prey and extends its pedipalps and legs I and (often) II out to contact and pin down the prey against the substrate. Legs III and IV remain within the burrow. As the pedipalps and legs drag the prey inward toward the spider's body, the extended chelicerae (and fangs) flex downward against the prey to help secure it. The prey is then pulled down into the burrow and the door closes automatically behind. The strike duration (time from first door movement to contact with prey) of four filmed *Aliatypus* prey captures ranged from 0.03–0.13 s and averaged 0.06 s, while the seizure duration (time from end of strike to the beginning of the spider's retreat into the burrow with the prey) of the same captures ranged from 0.22–0.44 s and averaged 0.28 s.

Coyle (1986a) performed a study which indi-

cates that *Aliatypus* trapdoor entrances permit less effective foraging than *Antrodiaetus* collar doors. The presentation of a standard substrate vibration stimulus to capture-ready spiders revealed a significantly ($P < 0.05$) lower prey capture effectiveness (as measured by the percent of stimuli resulting in accurate strikes) for *Aliatypus* species (*A. californicus*, *A. isolatus*, and *A. thompsoni*) than for *Antrodiaetus unicolor*. Even though both taxa were about equally effective in responding accurately to stimuli presented at the ventral half of the entrance circumference and the response effectiveness of both was lower for dorsal sector stimuli, the propensity to strike, the strike accuracy, and the percent of stimuli resulting in accurate strikes at the dorsal sector of the entrance were significantly ($P < 0.01$) lower for *Aliatypus* than for *A. unicolor*. Apparently *Aliatypus* is programmed to be very reluctant to strike at substrate vibrations generated near the trapdoor hinge, probably because the hinge decreases the probability that such a strike will be successful and may be vulnerable to damage during such strikes.

Diet.—In most species of *Aliatypus* we found fragmented prey exoskeletons packed into the bottom end of many of the burrows we excavated. These trash deposits were up to 10 mm deep in some *A. gulosus* burrows (Fig. 50). Since hard exoskeletons were fragmented less and were thus easier to locate and identify than softer ones, it is probable that the following list of prey remains is greatly biased in favor of hard-bodied taxa. Beetles were the most common prey in these trash deposits; included were tenebrionids, carabids, weevils, coccinellids, and a flightless tiger beetle. Ants and isopods were the next most common taxa in these deposits. Fragments of isopods were especially abundant in *A. gulosus* burrows (Fig. 50) at Salt Creek. Ant remains were unusually plentiful in *A. janus* burrows at both Hume Lake and Mammoth Lakes. Twenty-six ant heads were packed into the bottom end of one of these adult female *A. janus* burrows. Other prey fragments found in *Aliatypus* burrows were those of parasitoid wasps, a hemipteran, a mutillid wasp, and a spider. Captive *Aliatypus* will consume a wide variety of insects; one immature male *A. janus* consumed 13 de-winged houseflies, two small Jerusalem crickets, one fruit fly, and a noctuid moth caterpillar during a six month period. The ability of a juvenile *A. californicus* male to survive in captivity without feeding for 18 months before resuming prey capture indicates that, like

many other mygalomorphs (Hutchinson 1904; Passmore 1933; Baerg 1958; Main 1987), *Aliatypus* spiders are adapted to survive for very long periods of food shortage, which may be particularly common during their long dry summers.

PREDATORS AND PARASITES

In spite of our failure to rear most of the parasitoids we collected to adulthood and to obtain species- or genus-level identifications of juvenile parasitoids and other potential predators or parasites, our studies show that pompilid wasps are among the most common enemies of *Aliatypus* spiders. Three *A. isolatus* spiders collected in the Santa Catalina Mountains on 7 July 1972 had each been attacked by pompilid wasps. Two of these spiders, whose burrows were only 15 cm apart, had been eaten, and their parasites had pupated in the bottom of the host's burrow. One of these wasps, a female pupa of *Aporus notabilis pulchritarsis* Cameron in her 19 mm long cocoon, matured later in captivity. The other wasp may have been killed by a hyperparasite (a chalcid wasp?), as evidenced by a small hole in the side of its cocoon. The third spider, an antepenultimate or penultimate male, was found halfway down its burrow and was paralyzed with a pompilid larva attached to its abdomen. At Fallbrook, six uninhabited burrows, at least some of which belonged to *A. plutonis* spiders, each contained a 12–15 mm long cocoon from which a pompilid wasp had emerged. Similarly, within a 2 × 3 m area at Salt Creek in November, three medium sized burrows, at least one of which belonged to an *A. gulosus* spider, each contained an empty pompilid cocoon. At Mount Diablo on 10 June a 12 mm long pompilid cocoon was found in the bottom of a burrow with the remains of an *A. erebus* spider. Sometime before 26 September a bombiliid fly pupa cut its way out of this cocoon, presumably using the horn-like projections on its head to make an exit opening quite similar to those which pompilid wasps cut with their mandibles. Although this pupa died before molting, it was identified as belonging to the subfamily Exoprasopinae, probably the genus *Villa*.

Parasitoid flies of the acrocerid genus *Eulonchus* appear to be equally important enemies of *Aliatypus* spiders. An acrocerid larva is recognizable as a large cream-colored oblong object visible through the living host's abdominal integument, usually on one side near the book lungs. The host's abdomen is typically not distorted until the larva is about to emerge. In October of

1970 the Alum Rock Park population of *A. californicus* hosted within a 2 × 6 m area a rather dense population of acrocerid flies, at least some of which were the metallic blue species *Eulonchus tristis* Loew. Each of seven small to medium sized juvenile spiders hosted an acrocerid larva appearing to occupy about one-half of its abdomen; three other medium sized burrows contained acrocerid pupal exoskeletons; and another much larger burrow (probably that of an adult female) contained parts of an adult *E. tristis*. An acrocerid larva was found in the abdomen of a juvenile *A. janus* in October at Mammoth Lakes at an elevation of 2650 m. Four Nevada City *A. erebus*, three juveniles and one adult female, were collected within a 6 × 6 m area in early October each with an acrocerid larva in its abdomen. When these spiders were kept in captivity, the larva killed the adult female and emerged and pupated on the wall of her burrow in mid-February, and the adult *Eulonchus* fly (very pubescent and with a long proboscis, a metallic green thorax, and a metallic purple abdomen) emerged from the pupal skin on 7 March. The three juvenile spiders and their parasitoid larvae died within a few weeks of capture but one of these spiders was able to construct a burrow and trapdoor and capture prey before it died. An adult female *A. trophonius* collected near Soquel in October, its abdomen nearly filled with an acrocerid larva, was kept alive in captivity for a year before it died; the larva did not emerge. Our observations are consistent with a pattern of springtime emergence for *Eulonchus* adults in California; emergence at this season would avoid the problem of emerging from plugged host burrows and facilitate the finding of flowers by these nectivorous flies. To date, *Eulonchus* species are only known to attack *Aliatypus*, *Antrodiaetus*, and *Atypoides* species as well as the crytauchenid trapdoor spider genus *Aptostichus* (Coyle 1971; Schlinger 1987; Vincent 1986).

Some evidence implicates additional *Aliatypus* enemies. Some mites were observed in the thoracic grooves of two *A. californicus* adult females 4.5 mi N Soquel in early August by the first author, but since these mites have been lost, it is not known whether they are parasites or commensals. A 5 mm long larva, which was identified as an asilid fly but has since been lost, was found beside the shriveled abdomen of a recently molted dead adult male *A. thompsoni* in the bottom of its burrow on 2 October at Chatsworth, suggesting that the larva may have attacked and

fed upon the especially vulnerable male. An abundance of small mammal burrows and the associated destruction of the burrows of *A. janus*, *A. erebus*, and other mygalomorphs at Pinehurst suggest that burrowing gophers, mice, moles, or shrews may seriously damage *Aliatypus* burrows or even eat the spiders. *Aliatypus* males wandering (nocturnally?) in search of receptive females are vulnerable to certain nocturnal predators, especially other trapdoor spiders (including unreceptive conspecific females). Remains of two *A. janus* males were collected after one had been killed and eaten by a medium sized *Aptostichus* spider at Woodlake in November and the other by an adult female *A. janus* at Sequoia National Park in August. A recently dead male of *A. californicus* was found suspended in a *Latrodictus* web on a roadbank at Aukum in November. Dispersing *Aliatypus* spiderlings are probably often captured by other predaceous ground-dwelling arthropods, particularly older, juvenile, burrow-dwelling mygalomorph spiders, including conspecifics, as was observed by Decae (1986) for the trapdoor spider *Cyrtocarium cunicularium* Olivier.

DEFENSIVE BEHAVIOR

A secondary function served by entrance sealing behavior may be defense. The type B entrance closure (silk seal plus soil plug, Fig. 18g) might be an especially effective deterrent to some enemies. It is remarkable that although large numbers of *A. thompsoni* spiders have been collected, and some of these (16 juveniles and one male) in the Tehachapi Mountains and at Chatsworth had lost their trapdoors, no evidence of predation or parasitism has been found in this species. Perhaps this low incidence of predation and parasitism in *A. thompsoni* is, in part, the result of this species' almost total commitment to type B entrance sealing during the dry part of the year. In addition to serving as a physical barrier against parasitoids, the type C soil plug (Fig. 18e) might also deter pompilid wasp attacks by causing the burrow entrance chamber to resemble an empty bottom chamber.

Only two instances of door-holding defensive behavior have been observed in this genus, both involving *A. aquilonius*. When two brooding females were disturbed at their burrow entrances while in foraging posture, they pulled their doors shut (without drastically changing their posture) with the claws of legs I (and perhaps the pedipalps and/or legs II) gripping the undersurface

of the door edge at its ventral sector. Both spiders continued to hold their doors shut with surprising strength. Presumably this behavior evolved in concert with the comparatively tough and thick door and entrance rim of this species in response to selection exerted by a particular enemy or set of enemies. Defensive door-holding is rather common in other trapdoor spider taxa, which sometimes use their fangs (especially if the door is thick) instead of, or in addition to, the pedipalp and first leg claws (Coyle et al. 1992).

When a collector excavates an *Aliatypus* burrow, the spider retreats to the lower end. If second instar spiderlings are present, they also retreat and cluster around and below the female. During the latter stages of excavation, one typically finds the spider backed into the bottom of the burrow presenting the same aggressive defensive posture exhibited by other antrodiaetids (Coyle 1971) and mygalomorphs in general (Fig. 49). The spider faces up the burrow, tilts its cephalothorax upward, lifts legs I (and perhaps II), pedipalps, and chelicerae, spreads the chelicerae apart, and extends the fangs. If prodded, the spider strikes. In this defensive maneuver the otherwise vulnerable abdomen would seem to be protected, but the effectiveness of this defense remains to be tested. Our observations indicate that adult females, especially those with broods, are more likely to adopt this defense and to employ it with greater intensity than adult males and juveniles. However, not all brooding females exhibit this defense. When removed from its burrow, an individual either attempts to run away (not as fast as *Aptostichus* but faster than *Bothriocyrtum*) or remains motionless and may flex its legs under its body, a behavior which facilitates downslope rolling.

CONCLUSION

We agree with Wilson (1992) that "the major remaining questions of evolutionary biology . . . have to do with selection pressures from the environment as revealed by the histories of particular lineages. . .". Shifts in morphology, physiology, and/or behavior which allow lineages to enter new adaptive zones are particularly important events in generating biodiversity, but little is known about the course these shifts take, the conditions which foster them, or the mechanisms involved. The natural history of *Aliatypus* reveals an interesting suite of adaptations for life in the seasonally arid Mediterranean climate

of California and may consequently provide some insight into adaptive shifts.

The atypids, which are currently assumed to be the sister group (or part, along with the funnelweb meciobothriids, of the sister group) of the antrodiaetids (Raven 1985; Eskov & Zonshstein 1990; Coddington & Levi 1991), construct above-ground tubular (*Atypus* and *Sphodros*) and collar-shaped (*Calommata*) extensions of their burrow lining resembling the collar and turret entrances of *Antrodiaetus* and *Atypoides* and live in mesic habitats (Van Dam & Roberts 1917; Gertsch & Platnick 1980; Schwendinger 1990). Consequently, it is likely that *Aliatypus* arose from an ancestor which, like its sister group (*Antrodiaetus* and *Atypoides*), had collar-doors and lived in mesic habitats of the Arcto-Tertiary geoflora. *Aliatypus* may have arisen during the Miocene as, according to Axelrod (1973), the California climate became dryer and elements of the Madro-Tertiary geoflora moved north into this region from Mexico to replace the Arcto-Tertiary geoflora. Alternatively, *Aliatypus* may have arisen earlier in dry areas of Mexico and expanded northward to California with the Madro-Tertiary flora, but the absence of any *Aliatypus* records from Mexico weakens this hypothesis.

We believe that a key event permitting the proto-*Aliatypus* to utilize the summer-drought habitats of California that were apparently largely outside the tolerance limits of its ancestors was the evolution of a trapdoor entrance. Although we are not aware of any experimental evidence, there is a large amount of circumstantial evidence which suggests that trapdoors provide a tighter seal and therefore protect burrows from dryness, heat, and fires more effectively than do other entrance types like collar-doors (Coyle 1986a; Main 1986). Not only would we expect the closed *Aliatypus* trapdoor to seal in moisture better than the collapsed/folded plesiomorphic collar-door, but we also suggest that less moisture loss occurs during foraging periods from a trapdoor entrance, which is only cracked open while the spider waits for prey and automatically shuts after a capture, than from a collar entrance, which is wide open while the spider waits and often remains open for awhile after prey capture. By using appropriate equipment to measure water loss and temperatures (Pulz 1987; Humphreys 1987) in *Aliatypus* and *Antrodiaetus* burrows in nature and in the lab, these hypotheses could be tested rigorously in the manner of Coddington's (1988, 1990) homology approach and Baum and

Larson's (1991) phylogenetic methodology. In an environment with long dry seasons, occasional episodes of extreme drought, and periodic fires, the reduced foraging efficiency of trapdoor entrances is probably more than compensated for by their heightened protection. We agree with Mayo (1988), based on her study of door construction behavior, that the evolution of this trapdoor from a collar-door in the proto-*Aliatypus* probably involved a simple genetic change affecting an orientation control center in the nervous system. In other words, the putatively crucial evolutionary change in this major adaptive shift into an arid-adapted trapdoor niche was, we suspect, surprisingly quick and easy. It should be mentioned that the reverse change, the evolution of a collar entrance from a trapdoor entrance, should be just as easy, and has probably occurred in one mygalomorph group or another (Coyle 1986a; Coyle et al. 1992), but unless the concept of the antrodiaetid sister group changes to one that constructs trapdoors, the most probable polarity in the antrodiaetids is collar to trapdoor.

Judging from the natural history of its closest relatives (Coyle 1971), we suggest that this adaptive pioneer, the first trapdoor building *Aliatypus*, was partly preadapted for coping with aridity; it excavated deep burrows, it was able to survive without food for long periods, male emergence was triggered by wet weather, and it was long-lived and iteroparous. In addition to the evolution of a trapdoor, other adaptive behavioral changes which probably occurred during the adaptive shift, and which set *Aliatypus* apart from its sister genera, include 1) greater use of entrance sealing, particularly the use of silk plus soil plugs, 2) a tendency to line the burrow either with more silk or packed soil casing, 3) constructing the egg sac in the bottom of the burrow, 4) a shift in the mating season from late summer and early fall to late fall or winter, and 5) a shift to earlier spiderling dispersal (from spring to winter). Every one of these changes was, like the evolution of a trapdoor, probably the result of selection for avoidance of desiccation and heat stress during the long dry summers of California's Mediterranean climate. And all of these changes appear to involve simple quantitative shifts in duration, intensity, orientation, or timing of preexisting behaviors. While sharing most of its arid-adapted traits with the well-studied arid-adapted aganippine idiopid trapdoor spiders of western Australia (Main 1957, 1976,

1987), *Aliatypus* does lack one notable, apparently arid-adapted, aganippine trait, very large eggs.

Within the *Aliatypus* lineage, geographic variation and speciation have probably been facilitated by low vagility and the complex shifting mosaic of climates and habitats which has been an important cause of California's high biodiversity. This particularly low vagility may be largely a consequence of no aerial dispersal and the burrow-bound life style of these spiders. It is noteworthy how similar the geographic distribution pattern of *Aliatypus* species is to that of other Californian taxa with low vagility and fossorial winter-active life-styles, like the salamanders of the genus *Batrachoceps* (Yanev 1980). The minor adaptive radiation within *Aliatypus* has generated a set of species adapted to a considerable range of habitat types and climates. Some species (*A. plutonis*, *A. torridus*, *A. gulosus*, and *A. thompsoni*) have invaded particularly dry habitats, others (*A. janus* and *A. isolatus*) have adapted to high elevation cold winter habitats, and the smallest bodied species (*A. gnomus*, *A. aquilonius*, and *A. trophonius*) seem to have specialized in the most mesic (but still summer-dry) habitats. This is only a beginning of what needs to be known; many of the morphological, physiological and behavioral traits which explain the fitness advantages of these species in these particular habitats will not be apparent without further study.

We have proposed in this paper many hypotheses about the functions of such traits; they all require testing. Many questions, like the few which follow and others posed earlier, beg further study: 1) Why are some burrow design features, like mode (and thickness) of entrance sealing, highly plastic within species, while others, like adult female door shape, not so variable? 2) Does small body size – which has apparently evolved three different times in the genus (Coyle 1994) and should be a handicap in dry habitats and tends to reduce clutch size – boost fitness by reducing the age at reproduction and thus the likelihood of reproducing? 3) Have no foraging specializations (which would reduce niche overlap) evolved in any of these species, and, if not, could this be a key reason why syntopy of *Aliatypus* species is rather rare? We believe that three key aspects of the biology of all *Aliatypus* species are particularly worthy of immediate study: 1) geographic and habitat distribution, 2) courtship and mating, and 3) life cycle. We invite

others to continue the study of these remarkable spiders.

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